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## MADROÑO

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## EFFECTS OF FIRE ON THE REPRODUCTIVE BIOLOGY OF *AGAVE PALMERI* (AGAVACEAE)

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### ABSTRACT

Fire is an important management tool that is used increasingly to restore natural composition, structure, and processes in semi-arid grasslands, woodlands, and forests of the southwestern U.S. I investigated the effects of fire on floral resources, fruit and seed set, and survivorship of *Agave palmeri*, an important food source of the endangered lesser long-nosed bat. Nectar production and sugar concentration, pollen and nectar standing crops, and fruit and seed production were measured in flowering plants with leaves damaged by fire and compared with unburned plants at three sites in two different human-ignited fires. In general, no significant differences were found in total nectar production, nectar sugar concentration, standing pollen crops, or fruit and seed set between burned and unburned plants. Standing nectar crops were slightly smaller than total nectar production amounts, but large amounts of nectar and pollen remained available at dawn in both burned and unburned plants. Initial mortality measured across all size classes at one site was only 3.3%. Although levels of burn damage relative to plant size were quite variable, plants with greater damage (61–100%) tended to be <0.6 m in height and diameter. These results indicate that fire did not appreciably decrease food resources of the lesser long-nosed bat or the reproductive resources and survivorship of *A. palmeri*. The rocky, low fuel habitats preferred by *A. palmeri* combined with certain morphological and physiological adaptations of the plant, such as a rosette shape and storage of accumulated carbohydrates in the center of the rosette, appear to protect the majority of stored resources within the plant's center during fire events.

Key words: *Agave palmeri*, fire, *Leptonycteris curasoae yurbabuenae*, lesser long-nosed bat.

### INTRODUCTION

*Agave palmeri* Engelm. is a perennial, rosette-shaped leaf succulent, and is widespread in desert scrub, oak savanna, and oak woodland communities of the Southwest Borderlands: the international four-corners area of Arizona, New Mexico, Sonora, and Chihuahua. Prescribed fire is one management tool that is being tested to control the conversion of grasslands into shrubland communities, to reduce high fuel loads in woodland communities, and to return communities of the Southwestern Borderlands to pre-settlement states (Allen 1996; Edmins-ter 1996). Although the pollen and nectar of *A. palmeri* are major food sources of the endangered lesser long-nosed bat (*Leptonycteris curasoae yurbabuenae*) (Hayward and Cockrum 1971; Howell 1972; Howell and Roth 1981; Slauson 2000), little is known about the effects of fire on *A. palmeri*, and in particular, on its production of food resources for floral visitors.

*Agave palmeri* has a prolonged juvenile period that may last 20–40 years, during which time water and carbohydrates accumulate in the leaves. Once maturity is reached, plants are monocarpic, flowering only once and then dying. Mature plants range in size from 0.5–1.6 m tall and 0.5–2.5 m wide with 56–124 leaves (Noble and Smith 1983; Slauson 2000). The inflorescence, or flowering stalk, is a large, open panicle that varies from 2–8 m in height with 10–30 umbels (flower cluster on side branch of inflorescence) (Slauson 1996; Hodg-

son 1999), and produces on average 1500–2200 flowers over the flowering season (Slauson 2000). Anthers are sizeable (8.7–20 mm in length) and produce large amounts of pollen if not removed on the night of dehiscence by bats, moths, or rain; pollen is usually harvested the following morning by various bees (Slauson 2000). Flowers secrete nectar nocturnally over a 6-day flowering period and produce an average of 2.5 ml of total nectar, with peak production on the second day (Slauson 1999, 2000). These large quantities of pollen and nectar attract many animals (Slauson 2000), including the lesser long-nosed bat. Nocturnal visitors have the “first crack” at pollen and newly secreted nectar.

The lesser long-nosed bat was federally listed as endangered in 1988 due to apparent low and declining numbers, disturbance of roosts, and an interdependence with its food resources (Shull 1988), but its status as endangered is controversial (see Cockrum and Petryszyn 1991). Several species of columnar cacti and agaves provide a “nectar corridor” for the lesser long-nosed bats, from spring as they migrate north from Central America and Mexico, through fall when they return to southern roosts (Gentry 1982; Fleming et al. 1993). In late July and early August, substantial numbers of lesser long-nosed bats migrate to higher elevations in southeastern Arizona (Cockrum 1991) where their primary food source from July through September is *A. palmeri* (Howell 1972; Howell and Roth 1981). In describing this mutualistic relationship,

Howell and Roth (1981) suggested that *A. palmeri* was also "strongly dependent" upon the lesser long-nosed bat for pollination. More recently, Slauson (2000) has shown that this mutualistic relationship is asymmetrical; bats depend on this agave species part of the year for food, but *A. palmeri* does not require bats for adequate sexual reproduction.

Episodic fires were common throughout most ecosystems of the Southwest Borderlands for at least 300–400 years prior to ca. 1900 (Baisan and Swetnam 1990; Swetnam and Baisan 1996a, b), including those occupied by *A. palmeri*. Kaib (1998) has shown desert grasslands burned approximately every 5–10 years, and ranged between 10 to hundreds of km<sup>2</sup> in size, while canyon pine-oak forests burned every 5–9 years and covered areas of at least 50 km<sup>2</sup>. A drastic reduction of these widespread, episodic surface fires occurred north of the border between ca. 1870–1900, initially as a result of intensive grazing that decreased fuels and the ability of fire to spread across large landscapes (Bahre 1991; McPherson et al. 1993; Allen 1996; Swetnam and Baisan 1996a, b). Continued grazing, land use, and fire suppression practices by government agencies throughout the 20th century resulted in the virtual extinction of natural disturbance fires in southwest ecosystems (Bahre 1991; Allen 1996; Swetnam and Baisan 1996a). These practices have contributed to many changes in both the structure and function of these communities, ranging from shrub invasion of desert grasslands due to a lack of fine fuels to carry low intensity fires (Hastings and Turner 1965; Humphrey 1987; McPherson 1995), to severe risk of catastrophic and stand-replacing wildfires in forests due to great fuel accumulations (Cooper 1960; Covington and Moore 1994).

Many succulents tolerate fire to some degree (Thomas and Goodson 1992), but desert grassland fires have also been reported to kill succulent plants (Niering and Lowe 1984; Nobel 1988), particularly the smaller size classes. McLaughlin and Bowers (1982) reported that large succulent plants that initially survived fires had increased mortality in later years. Several other factors besides plant size may affect the responses of succulents to fire including the size and patchiness of the fire, the time of year fire occurs, fuel conditions, weather conditions, topography, and plant morphology and physiology (McPherson 1995). Little data are available regarding the effects of fire on agaves. In simulated grassland fire experiments, *A. gigantensis* had 0% mortality after 14 months with fuel densities up to 1600 g m<sup>-2</sup> and temperatures of 400–600°C (these temperatures are normally expected in intense grassland fires) (Thomas and Goodson 1992). Although the leaf tips collapsed at fuel densities of 400 g m<sup>-2</sup> and damage increased as fire intensity increased, the center of the rosettes remained unburned. In field surveys of semi-desert grassland sites in southern Arizona that had burned in wildfires in the

prior 18 months, mortality from fire was 18% in *A. palmeri* (Thomas and Goodson 1992). Of the remaining living plants, 83% exhibited regrowth from the apical meristem, whereas 17% survived unburned in refugia. These refugia were created by either the patchy nature of the fire, which skipped over areas with adequate fuels, or by rocky areas with little flammable material.

The prolonged juvenile period of agaves results in large amounts of stored resources that are used for flower (including nectar and pollen), fruit, and seed production. Once flowering is initiated, a large and irreversible translocation of stored resources occurs from the rosette to the developing inflorescence. Death results presumably because resources normally reserved for growth and maintenance are mostly allocated to reproduction. Nobel (1977) observed that *A. deserti* Engelm. diverted over 68% of its stored biomass to a developing inflorescence. No data are available regarding how the loss of stored resources from fire damage in reproductive agaves affects nectar and pollen production or subsequent fruit and seed set.

*Research questions.* I studied aspects of the floral biology of *Agave palmeri* relevant to nectar bat visitation immediately following two summer fires. These fires, one prescribed and one accidental, burned patchily and caused little immediate mortality of mature agave plants. Plants that were reproductive the year of each fire had partially or fully emerged inflorescences at the time of the fires, and either were flowering or flowered soon after. I compared reproductive burned plants with unburned plants and asked (1) did nectar production rate or concentration differ between the two treatment classes? (2) What was the standing crop of nectar and pollen at dawn, after possible bat visitation? (If floral rewards of populations were closely cropped by bats, then an adverse effect of burning on nectar production would be important. A surplus in both nectar production and standing crops would indicate that floral foods were not in limited supply for nocturnal visitors. Differences between burned and unburned plants could indicate production differences or discrimination by nocturnal visitors.) (3) Did fruit and seed set differ between burned and unburned plants? (A significant decrease in fruit or seed set could have considerable impacts on future floral resources for bats.) (4) Was burn damage of plants related to their size, specifically the height and diameter of the rosette?

## METHODS

*Study sites.* Fieldwork was conducted at two different fire sites, a prescribed burn and an accidental human-ignited fire. The prescribed burn (known as the Maverick Burn) was conducted on June 24–25, 1997 by the U.S. Forest Service on the southern edge of the Peloncillo Mountains (Fig. 1). Approximately 8000 acres burned in a mosaic pattern with-

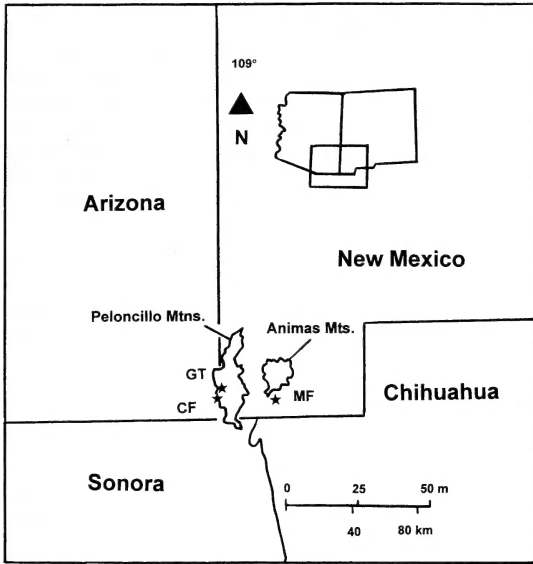


FIG. 1. Locations of CF, GT (Maverick Burn), and MF (Gray Ranch) study sites.

in the 17,000 acres designated as the primary burn area (Encinas 1997). Two study sites were chosen within the primary burn area that represented typical habitats for *A. palmeri* (Gentry 1982). The first study site was located in the southern portion of the burn area on Cowboy Flats (CF site, lat  $31^{\circ}26'N$ , long  $109^{\circ}2'W$ , elevation  $\sim 1585$  m) near a small lesser long-nosed bat roost. This site was on a rocky, south-southwestern facing hillside and mesa top in an oak savanna community. Plant species composition included *Quercus emoryi*, *Q. oblongifolia*, *Juniperus monosperma*, *Prosopis velutina*, *Yucca schottii*, *Nolina microcarpa*, *Dasyllirion wheeleri*, *Fouquieria splendens*, *Calliandra* sp., *Gutierrezia sarothrae*, *Bouteloua gracilis*, *B. curtipendula*, *B. hirsuta*, *B. radicata*, *Hilaria belangeri*, *Eragrostis intermedia*, *Muhlenbergia* sp., *Lycurus phleiodes*, *Aristida* spp., *Schizachrium cirratum*, and *Heteropogon contortus*. The second study area was located along the northern border of the burn area along Geronimo Trail (GT site, lat  $31^{\circ}32'N$ , long  $109^{\circ}2'W$ , elevation  $\sim 1675$  m), and was characterized by flat to steep ( $0$ – $45^{\circ}$ ) slopes with south-southwestern exposures and rocky soils in an oak savanna/oak woodland community. Plant species included *Q. emoryi*, *Q. oblongifolia*, *J. monosperma*, *J. deppeana*, *P. velutina*, *Arctostaphylos pungens*, *Y. schottii*, *G. sarothrae*, *B. gracilis*, *B. curtipendula*, *B. hirsuta*, *B. radicata*, *H. belangeri*, *E. intermedia*, *Aristida* spp., *S. cirratum* and *M. emersleyi*.

The accidental human-ignited fire started in Mexico in May 1999, crossed the international border, and burned approximately 22,000 acres in a mosaic pattern over a 2-day period on the Gray

Ranch in southeastern New Mexico (Fig. 1). The third study site was located on the Gray Ranch near McKinney Flats (MF site, lat  $31^{\circ}23'N$ , long  $108^{\circ}42'W$ , elevation  $\sim 1570$  m) on a south-facing, rocky slope in a semi-arid grassland/oak savanna community. Plant species included *Q. emoryi*, *Q. oblongifolia*, *P. velutina*, *N. microcarpa*, *Juniperus* sp., *Cylindropuntia spinosior*, *G. sarothrae*, *B. gracilis*, *B. curtipendula*, *B. hirsuta*, *B. radicata*, *H. belangeri*, *Aristida* spp., and *S. cirratum*. Agave populations (all size classes excluding seedlings) at study sites ranged from approximately 1000–3000 plants per ha.

Although several plots were identified as potential study sites prior to the Maverick fire, ignitions were initiated across broad landscape areas rather than igniting individual study plots, and none of the potential study plots burned. Therefore, thorough pre-treatment characterization of plots was not possible. Due to the large areas of steep and inaccessible terrain, the mosaic pattern of the fire, the patchy distribution of agaves, and limitations of sampling nectar and pollen with 12-foot ladders, only two suitable sites that actually burned could be located within the primary burn area. At these sites, fire behavior was characterized by partial to complete understory consumption (Clark 2000). The Gray Ranch fire was accidental, and only one accessible agave population burned.

Research was conducted at both fire sites during late July and August during the peak flowering period of *A. palmeri* and when migrating lesser long-nosed bats are normally present in southeastern Arizona. Work was conducted August 4–9, 1997 at the CF site, August 11–15, 1997 at the GT site, and July 20–22 and August 2–4, 1999 at the MF site.

**Nectar and pollen studies.** I studied nocturnal nectar production in bagged, or enclosed, flowers to determine whether this important floral reward was affected by fire. I also measured standing crops of nectar and pollen at dawn in unbagged, or open, flowers. Standing crops reflect both the effects of harvesting by animals and production of floral rewards by flowers. Plant selection was limited to plants whose flowers could be reached with 12-foot ladders in burned and unburned areas at each site. A plant was classified as a "burned plant" if  $>1\%$  of the rosette had tissue death due to fire. Rosette height, width, and number of umbels were measured for each study plant. For study plants in burned areas, burn damage (% of rosette damaged by fire) was scored from 0 to 6: 0 = no burn damage, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%, and 6 = entirely dead.

Sample sizes for nectar and pollen studies at all sites were restricted due to the mosaic pattern of the fire, the patchy distribution of agaves on primarily inaccessible and rocky terrain, and the number of plants in flower that could be reached with 12-foot ladders. In general, all plants that could be

reached at a site were sampled. Total nectar production, nectar sugar percentage, and standing nectar and pollen crops were measured on six plants each in burned and unburned plots at the CF site and nine plants at the unburned GT site. Flowers on most plants in the burned GT plot were too high to reach with ladders, and only 2–3 plants could be sampled, depending on the day and appropriate flower stage availability. At the MF site, 20 and 10 plants were measured in the burned and unburned plots, respectively. To decrease any positional effects of nectar volume, nectar sugar concentration or standing crops, experimental flowers were located on umbels positioned in the middle section of the inflorescence, whenever possible.

For studies of total nectar production and nectar sugar concentration at the CF and GT sites, 5–10 predehiscent (day 1 of 6-day flowering period) flowers on one umbel were numbered, enclosed with a nylon mesh bag prior to dusk, and nectar was allowed to accumulate until dawn (nectar is produced only during the night). Anthers of predehiscent flowers generally split open and dehiscid pollen shortly after dusk, entering the dehiscent (day 2) floral stage. Dehiscent stage flowers were used in nectar and pollen experiments as nectar production is greatest in dehiscent flowers, and pollen is only available during the dehiscent stage (Slauson 2000). Plants were sampled for three successive days for total nectar production studies (different flowers sampled each day) and one day for nectar sugar concentration studies. Nectar production was measured by withdrawing the nectar present in the floral tube at dawn with a tuberculin syringe and blunt end needle. Nectar sugar concentration (percent sucrose equivalents on a weight/weight basis) was measured in the field at dawn with a hand-held refractometer. Data collection methods for total nectar production and nectar sugar concentration were modified for the MF site in an attempt to increase the number of plants sampled for comparison to standing nectar crops (see below). Plants were sampled one day only and data collection was spread over a 3-day period (4–7 plants per treatment were sampled each morning at dawn). To determine if nectar resources decreased significantly over time, total nectar production and nectar sugar concentration measurements were repeated on the same study plants two weeks later (August 2–4, 1999). Due to the difference in sampling methodology, fire sites were analyzed separately.

To indirectly determine the degree of nectar use by nocturnal floral visitors (bats and moths), standing nectar crops (amount of nectar present at dawn in flowers left available to visitors) were measured and compared to total nectar production (exclosed flowers) at all three study sites. In order to most accurately measure dawn standing crops, sampling was begun as close to dawn as possible (<one hour), and was completed before dawn when an abundance of bees and other diurnal animals ap-

peared that could substantially decrease standing nectar amounts. Standing crops were measured on umbels adjacent to those used for studies of total nectar production and nectar sugar concentration. Nectar volume was sampled on three successive days and nectar concentrations were sampled one day on 5–10 dehiscent flowers per plant at the CF and GT sites. Methodology differed at the MF site; standing nectar crops and nectar sugar concentrations were measured on 4–7 plants (five dehiscent flowers per plant) each morning at dawn during the first sampling period (July 20–22). Nectar and nectar sugar concentrations were measured as previously described.

Standing pollen crops (amount of pollen present at dawn in flowers left available to visitors) were measured using a qualitative 5-class index at all 3 sites to estimate pollen resource use by nocturnal floral visitors. Standing pollen crops were measured by evaluating the amount of pollen present at dawn and scoring pollen from 0 to 5 (0 = no pollen present, . . . , 5 = all or large amounts of pollen present). At the CF and GT sites, standing pollen crops were measured on umbels adjacent to those used for total nectar production and nectar sugar concentration studies. Five to ten dehiscent flowers per plant were sampled for three successive days (different flowers sampled each day). At the burned GT site, low numbers of available flowers and inability to reach flowers with ladders allowed sampling on only two plants (one plant sampled for one day and one plant sampled for two days). Methodology differed at the MF site; plants were sampled one day only and data collection was spread over a 3-day period (4–7 plants per treatment were sampled each morning at dawn).

*Fruit and seed set studies.* To determine whether fire significantly effected fruit and seed set of agaves, 12 plants each from burned and unburned sites at the CF and GT sites, and 20 plants from the burned and 22 plants from the unburned MF site were randomly selected by a coin toss after the fire. Plants were allowed to be open-pollinated, stalks were cut down, fruits were collected in October and November, and mean percent fruit and seed set for each inflorescence were calculated. To determine fruit set, the total number of mature fruits and aborted flower scars on each inflorescence were counted, and percent fruit set was calculated (number of fruits/(number of fruits + aborted flower scars)). Mean seed set per plant was determined by placing all fruits of an inflorescence in a paper bag, randomly selecting 20 fruits, and calculating seed set for each fruit (number of black, fertilized seeds/(number of black, fertilized seeds + number of white, unfertilized ovules)). Capsules had dehisced in several inflorescences prior to fruit collection, so seed set could only be measured on only six plants each in burned and unburned plots at the CF site, six plants in the burned GT plot, eight plants in the

TABLE 1. MEAN PLANT SIZE AND BURN DAMAGE  $\pm 1$  SE OF REPRODUCTIVE *A. PALMERI* USED IN NECTAR AND POLLEN STUDIES AT CF, GT, AND MF SITES. RH = rosette height (m), RW = rosette width (m), BD = burn damage estimate (0 = no burn damage, 1 = 1–20% of rosette burned, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%, 6 = dead). Values with different superscripts were significantly different ( $P < 0.02$ ) within study sites.

	Site	RH (m)	RW (m)	BD
Burned	CF (n = 6)	0.93 $\pm$ 0.04	1.48 $\pm$ 0.10	2.6 $\pm$ 0.6
	GT (n = 3)	1.13 $\pm$ 0.09 <sup>a</sup>	1.46 $\pm$ 0.09	3.3 $\pm$ 1.2
	MF (n = 14)	0.79 $\pm$ 0.04	1.19 $\pm$ 0.08	1.6 $\pm$ 0.2
Unburned	CF (n = 6)	0.88 $\pm$ 0.05	1.32 $\pm$ 0.12	—
	GT (n = 9)	0.82 $\pm$ 0.05 <sup>b</sup>	1.25 $\pm$ 0.09	—
	MF (n = 10)	0.77 $\pm$ 0.05	1.19 $\pm$ 0.08	—

unburned GT plot, 15 plants in the burned MF plot, and 16 plants in the unburned MF plot.

*Mortality and demography studies.* To examine agave demography and mortality from fire, four 20  $\times$  50 m plots were established within the burned area at one fire site (MF site) after the fire. Fire severity appeared relatively uniform within the burned area, and was not considered in plot location. Azimuth (degrees) and direction (m) to the plots from the road that divided the burned and unburned areas were selected from a random numbers table. All plants within plots were tagged, rosette height and diameter were measured, survivorship and reproductive status noted, and degree of burn damage (as previously described) recorded.

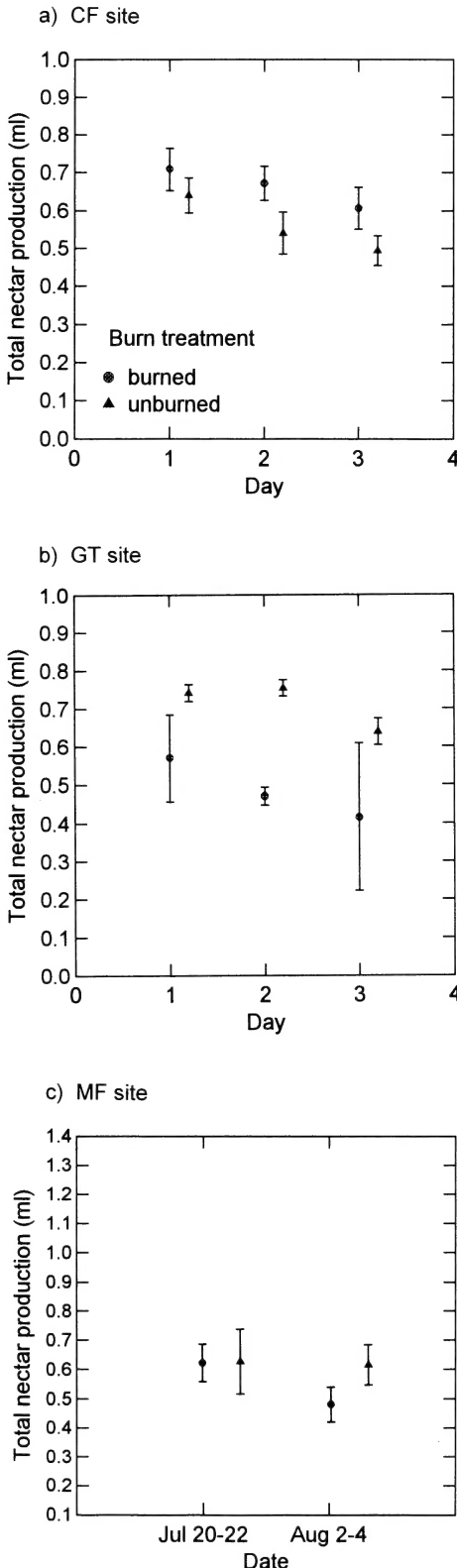
*Data analysis.* Total nectar production, standing nectar crop, and exclosed nectar sugar concentration data had normal distributions, variances, and residuals at all three study sites, and were analyzed by one-way repeated measures ANOVA (plants = repeated measure). Sample size in burned plants for total nectar production and nectar sugar concentration studies was reduced to 14 as six plants were either finished flowering or flowers could not be reached during the second sampling period (August 2–4). Standing nectar crop data for the burned GT plot were excluded from the analysis as no flowers were available for measurement on several plants on various days. Due to the small number of plants with paired data values for standing nectar sugar concentrations ( $n \leq 4$  plants per treatment) for the CF and GT sites, data were analyzed by the Proc Mixed procedure of SAS (SAS 1999) which uses maximum likelihood estimation procedures to handle missing data in repeated measures analysis. Fruit and seed set data had normal variances, distributions, and residuals, and were analyzed by one-way ANOVA. All statistical analyses were performed using SYSTAT 9.01 (SPSS Inc. 1999) unless otherwise noted.

RESULTS

*Burn damage and size of nectar plants.* Damage to burned agaves used for nectar studies ranged from a mean score of 1.6 (1–20% of rosette burned) at the MF site to 3.3 (41–60% of rosette burned) at the GT site (Table 1). Differences between sites were not significant (Kruskal-Wallis test,  $K/W = 3.14$ ,  $P = 0.206$ ), but sample size was low for the GT site ( $n = 3$ ). In general, plants from the MF (Gray Ranch) site were smaller than those from the CF and GT sites. Burned plants were significantly taller than unburned plants at the GT site (one-way ANOVA with Bonferroni adjustment,  $F_{1,10} = 7.614$ ,  $P = 0.02$ ). Number of umbels per inflorescence ranged from 16–23 among sites.

*Nectar, nectar sugar concentration, and pollen production.* Mean nectar production did not differ greatly between burned and unburned plants, but results were variable between sites, and occasionally between plants. Total nectar production was significantly higher in burned plants at the CF site (one-way repeated measures ANOVA,  $F_{1,10} = 6.366$ ,  $P = 0.03$ ) (Fig. 2a), and a significant linear decrease in nectar production was observed over the three-day period (one-way repeated measures ANOVA,  $F_{1,10} = 7.740$ ,  $P = 0.019$ ). At the GT site where burn damage was greater (3.3, or 41–60% of rosette burned), mean nectar production was significantly lower in burned plants (one-way repeated measures ANOVA,  $F_{1,6} = 19.184$ ,  $P = 0.005$ ) (Fig. 2b), however, sample sizes were very small for the burned site ( $n = 3$  plants). Nectar production was also observed to significantly decrease linearly over the three-day period (one-way repeated measures ANOVA,  $F_{1,6} = 11.040$ ,  $P = 0.016$ ). At the MF site, no significant differences in total nectar production were found between burned and unburned plants during either sample period (July 20–22 and Aug 2–4, Fig. 2c) (one-way repeated measures ANOVA,  $F_{1,22} = 0.662$ ,  $P = 0.425$ ), although nectar





production did decrease slightly over time, but not significantly (one-way repeated measures ANOVA,  $F_{1,22} = 2.993$ ,  $P = 0.098$ ).

Dawn nectar sugar concentrations of enclosed flowers were significantly higher at the CF site (mean  $\pm$  SE =  $20.6 \pm 0.9\%$ , range 17–27%) than the GT site (mean  $\pm$  SE =  $17.5 \pm 0.4\%$ , range 15.5–19%) (one-way ANOVA,  $F_{1,8} = 7.02$ ,  $P = 0.029$ ). Although burned plants (mean  $\pm$  SE =  $19.8 \pm 1.3\%$ ) tended to have slightly higher sugar concentrations than unburned plants (mean  $\pm$  SE =  $18.7 \pm 0.7\%$ ), differences were not significant (one-way ANOVA,  $F_{1,8} = 0.56$ ,  $P = 0.475$ ). At the MF site, dawn nectar sugar concentrations of enclosed flowers ranged from 12.7–18.8% (Jul 20–22 mean  $\pm$  SE =  $16.1 \pm 1.2\%$ , Aug 2–4 mean  $\pm$  SE =  $14.6 \pm 1.7\%$ ). Sugar concentrations were not significantly different between burn treatments (one-way repeated measures ANOVA,  $F_{1,22} = 0.585$ ,  $P = 0.452$ ), but decreased significantly on the second sampling date (Aug 2–4) (one-way repeated measures ANOVA,  $F_{1,22} = 13.580$ ,  $P = 0.001$ ).

Pollen levels were not observed to vary between sites, burn treatment, or over time at all three study sites. Only one burned plant at the GT site and one unburned plant at the CF site were observed to differ from a pollen score of 5, and then only for one sampling time.

*Standing nectar and nectar sugar concentration crops vs. total nectar production.* Standing nectar crops were lower than total nectar production, but significant amounts of standing nectar ( $>0.54$  ml) were available at dawn at all sites. A significant interaction was present in nectar production between the burn treatment and standing nectar crop vs. total nectar production at the CF site (one-way repeated measures ANOVA,  $F_{1,10} = 5.765$ ,  $P = 0.037$ ), and as nectar production was averaged across the burn treatment, it was not advisable to interpret the standing crop vs. total nectar production test. Data were subsequently analyzed by running paired t-tests on standing nectar crop and total nectar production data by burn treatment. Standing nectar crop (mean  $\pm$  SE =  $0.565 \pm 0.033$  ml) was significantly lower than total nectar production (mean  $\pm$  SE =  $0.662 \pm 0.027$  ml) in burned plants (t-test,  $t = -1.767$ ,  $P = 0.017$ ,  $\alpha/2$  (0.025) to maintain Type I error), but no significant difference was found in nectar production between standing nectar crop (mean  $\pm$  SE =  $0.546 \pm 0.029$  ml) and total nectar production (mean  $\pm$  SE =  $0.558 \pm 0.028$  ml) in unburned plants (t-test,  $t = -0.244$ ,  $P = 0.646$ ,  $\alpha/2$  (0.025) to maintain Type I error). At the GT site, no significant differences in nectar

FIG. 2. Mean total nectar production (ml) of dehiscent *A. palmeri* flowers in burned and unburned plots, (a) CF site, (b) GT site, and (c) MF site. Vertical lines = 1 SE.



production were found between standing nectar crop (mean  $\pm$  SE =  $0.612 \pm 0.031$  ml) and total nectar production (mean  $\pm$  SE =  $0.711 \pm 0.018$  ml) in unburned plants (one-way repeated measures ANOVA,  $F_{1,3} = 1.101$ ,  $P = 0.371$ ) or in nectar production between days (one-way repeated measures ANOVA,  $F_{2,6} = 3.927$ ,  $P = 0.081$ ). Data for standing nectar crop and total nectar production in burned plants were not analyzed due to low sample size ( $n = 2$ ) and missing paired data values (flowers were not available for both open and exclosed nectar production on all three nights for the three plants with flowers that could be reached). At the MF site, no significant differences in nectar production were found between burned and unburned plants (one-way repeated measures ANOVA,  $F_{1,28} = 2.764$ ,  $P = 0.108$ ) or standing nectar crop and total nectar production (one-way repeated measures ANOVA,  $F_{1,28} = 0.791$ ,  $P = 0.381$ ) (standing crop mean  $\pm$  SE =  $0.515 \pm 0.038$  ml, total nectar production mean  $\pm$  SE =  $0.557 \pm 0.042$  ml).

Nectar sugar concentrations of standing nectar crops ranged from 16.7–29.6% at the CF site and 16.2–21.9% at the GT site. Nectar sugar concentrations were significantly higher at the CF site (Proc Mixed procedure,  $F_{1,20} = 7.11$ ,  $P = 0.015$ ) and in standing crop flowers at both sites (Proc Mixed procedure,  $F_{1,7} = 8.70$ ,  $P = 0.021$ ) (CF site: standing crop mean  $\pm$  SE =  $21.8 \pm 1.1\%$ , total nectar production mean  $\pm$  SE =  $20.6 \pm 0.9\%$ ; GT site: standing crop mean  $\pm$  SE =  $19.2 \pm 0.6\%$ , total nectar production mean  $\pm$  SE =  $17.5 \pm 0.4\%$ ). At the MF site, standing nectar sugar concentrations ranged from 12.6–19.5%. No significant differences in nectar sugar concentrations were found between burned (mean  $\pm$  SE =  $15.8 \pm 0.3\%$ ) and unburned plants ( $15.0 \pm 0.5\%$ ) (one-way repeated measures ANOVA,  $F_{1,28} = 2.220$ ,  $P = 0.147$ ) or between standing nectar crop (mean  $\pm$  SE =  $15.6 \pm 0.3\%$ ) and total nectar production (mean  $\pm$  SE =  $15.5 \pm 0.2\%$ ) (one-way repeated measures ANOVA,  $F_{1,28} = 1.167$ ,  $P = 0.289$ ).

**Fruit and seed set.** Burned and unburned plants had similar levels of fruit (17–22%) and seed set (19–23%) (Fig. 3). No significant differences were found in fruit set between study sites (one-way ANOVA,  $F_{2,84} = 1.915$ ,  $P = 0.154$ ). Fruit set was somewhat lower in burned plots, but not significantly (one-way ANOVA,  $F_{1,84} = 0.294$ ,  $P = 0.589$ ). Seed set was slightly higher in two of the three burned plots, but differences were not significant (one-way ANOVA,  $F_{1,49} = 0.641$ ,  $P = 0.427$ ). Seed set at the CF site was significantly lower than the GT and MF sites (one-way ANOVA, Bonferroni test,  $P < 0.05$ ).

**Mortality and demography.** Overall mortality of plants in demography plots measured two months after the Gray Ranch fire (MF site) was 3.3% (Plot 1 = 4.6%,  $n = 194$ , Plot 2 = 2.5%,  $n = 355$ , Plot 3 = 3.9%,  $n = 276$ , Plot 4 = 3.0%,  $n = 459$ ). Mean

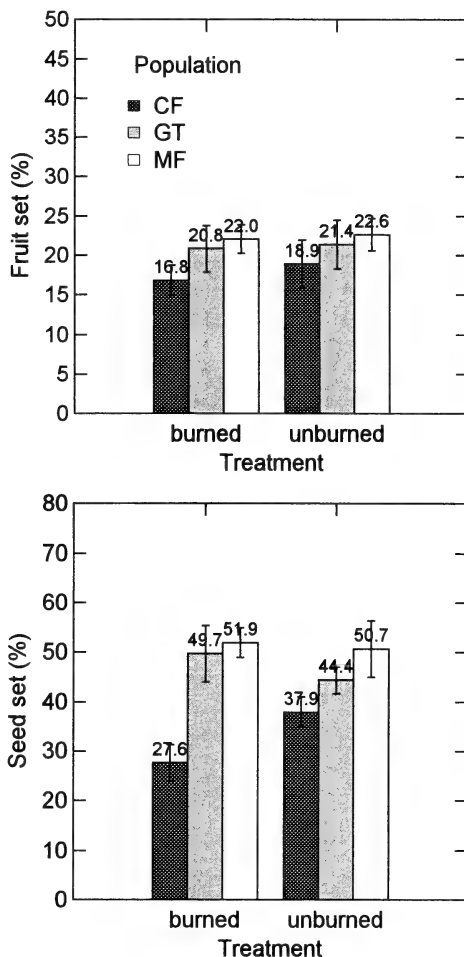


FIG. 3. Mean fruit and seed set (%) of *A. palmeri* in burned and unburned plots, CF, GT, and MF sites. Vertical lines = 1 SE.

burn damage  $\pm$  SE was  $3.1 \pm 0.03$  (41–60% of rosette damaged) (range of plots =  $3.4 \pm 0.06$  to  $2.7 \pm 0.05$ ) with approximately 37% of plants falling into this damage class (Fig. 4). Burn damage classes 4 (22% of plants) and 2 (16% of plants) were the next most frequent damage classes. A multinomial logit model (Agresti 1990) relating burn class damage to rosette height and width correctly predicted damage class for only 25% of observations. The variability in this relationship is shown in Figure 5. Although median plant size across all levels of burn damage did not differ greatly, the range was quite variable. Rosette height and width values associated with burn damage classes  $\geq 3$  were more concentrated than those of burn damage classes 1–2.

Rosette height and width size class distributions illustrate the relatively young age of the population (Fig. 6). Greater than 90% of the population was  $<0.3$  m in height and width.

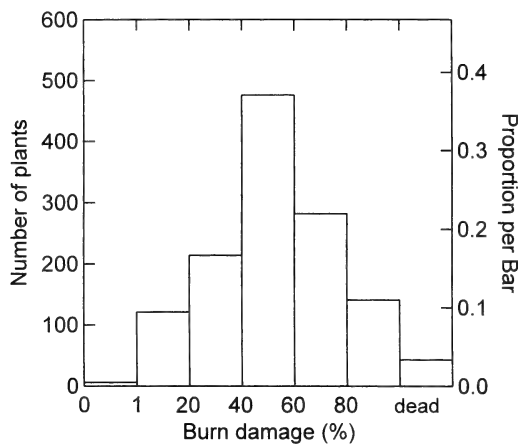


FIG. 4. Burn damage (% of rosette damaged by fire) of *A. palmeri* at the MF site. 0 = no burn damage, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%, 6 = dead.

DISCUSSION

Burning did not appear to negatively impact the production of nectar in *A. palmeri*. Mean total nectar production for all sites and times sampled (range  $\pm$  SE = 0.46–0.71  $\pm$  0.5 ml) was similar to or greater than previous reports of nectar production

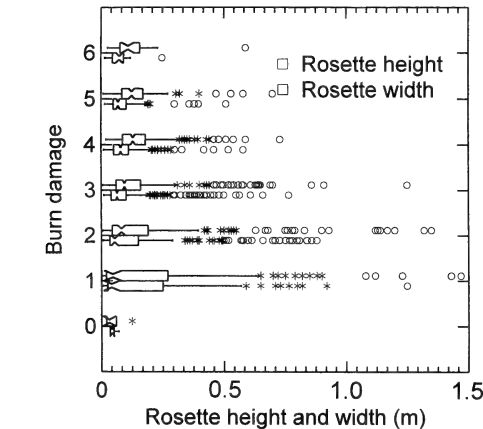


FIG. 5. Relationship between plant size (m) and burn damage (% of rosette damaged by fire) of *A. palmeri*, MF site. 0 = no burn damage, 1 = 1–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%, 6 = dead. Lower box plot of each pair indicates rosette height, upper box plot indicates rosette width. Length of box plot = range within 50% of values fall, center notch = median, box edges = first and third quartiles, whiskers = values within the first quartile – (1.5  $\times$  midrange) and the third quartile + (1.5  $\times$  midrange), asterisks = values between first quartile – (1.5 to 3.0  $\times$  midrange) and third quartile + (1.5 to 3.0  $\times$  midrange), and open circles = values <first quartile – (3.0  $\times$  midrange) and >third quartile + (3.0  $\times$  midrange).

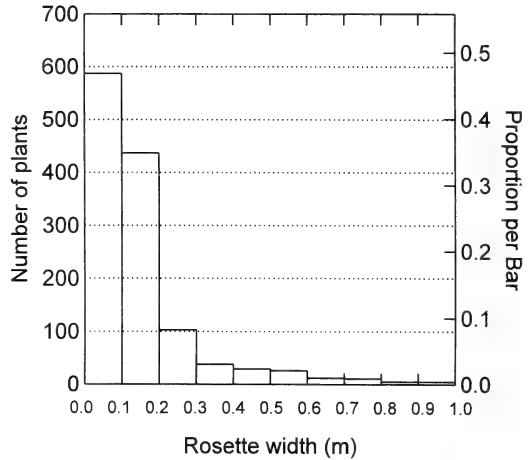
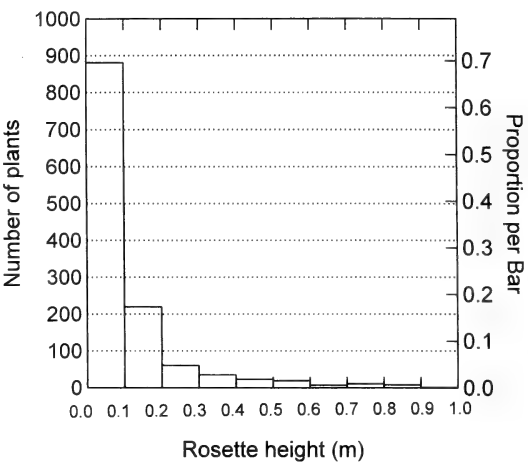


FIG. 6. Size class distribution of *A. palmeri*, MF site.  $n$  = 1298 plants.

in dehiscent flowers of unburned plants (Howell 1979; Slauson 1999, 2000). The significantly lower nectar production of burned plants at the GT site may be a result of sampling error due to the low sample size ( $n$  = 3 plants). Nectar sugar concentrations were not significantly different between burned and unburned plants at any site, and values were well within the range reported in previous studies of unburned plants (Howell 1979; Slauson 1999, 2000). Nectar production and nectar sugar concentrations decreased over time in both burned and unburned plants, and this trend suggests that nectar resources may naturally decrease during the flowering period as stored resources are depleted and fruit and seed production increase. Pollen production did not appear to be affected adversely as large amounts of pollen were present on anthers at dawn at all sites and sampling times.

Standing nectar crops at dawn were smaller than total nectar production in all treatments at all sites

(only significantly lower at the burned CF site), presumably as a result of nectar use by moths and bats. However, at all study sites large amounts of nectar ( $>0.54$  ml) and pollen (score = 5) were available in standing crop flowers at dawn, and indicate that food resource availability was not a limiting factor for either nocturnal (bats or moths) or diurnal visitors at any study sites during the times sampled. Standing crop results were similar to previous reports from other populations (Slauson 2000).

The study sites examined did not appear to contain the fuel loads required to support a fire of the intensity needed to kill mature (reproductive) agaves or cause significant initial mortality when all size classes were considered. Although the majority of the population was quite small in size at the MF site (Fig. 6), mortality was  $<4\%$ . Mean burn damage of mature plants was moderate at all sites (approximately 10–43% of rosette burned), and in no case did mean damage exceed class 3 (41–60% of rosette burned). Relatively few large, non-reproductive plants ( $>0.6$  m in height or diameter) had burn damage  $>60\%$  (Fig. 5), and mean burn damage of all size classes at the CF site was approximately 43%, despite the fact that over 90% of the population was  $<0.3$  m in height and diameter.

The low to moderate burn damage and high initial survivorship of agaves may be due in part to their preferred habitats. Agave populations of moderate to high densities are characteristically found in xeric sites with rocky soil surfaces where competition with other plants is low (Gentry 1982). These rocky, low fuel habitats may serve as a refugia from fire for some agaves, especially smaller agaves which may be protected near the bases of surface rocks and cobbles. Plants located in less rocky, denser grassland or woodland habitats with increased fuel loads would presumably sustain greater damage. The greater burn damage observed in plants at the GT site (41–60%) may have been due to larger amounts of available fuels present in the surrounding oak savanna and oak woodland community. Robinett and Barker (1996) noted that frequent seedling establishment of *A. palmeri* occurs around dried, dead adult plants, and fuel loads created by dead adults can produce intense heat in a fire that kills surrounding seedlings. The variability in the fuel loads of individual agave microhabitats most likely explains the unpredictability of burn damage as a function of plant size observed in this study, especially in the smaller size classes (Fig. 5).

Certain morphological and physiological adaptations may also lessen the effect of fire on agaves. A number of agave species may resprout from rhizomes after fire (Gentry 1972), although most populations of *A. palmeri* are not rhizomatous (Slauson personal observation). Agaves may also benefit from the release of nutrients after a fire due to their shallow root system (Gentry 1982). The rosette form of agaves to some degree protects the apical

meristem and the majority of stored resources located in the center of the plant. Reproductive agaves may have an even greater advantage: beginning in late winter and early spring, stored water and carbohydrates in reproductive agaves are translocated from the leaves to the center of the rosette where they are utilized for the development of the inflorescence (Nobel 1977; Tissue and Nobel 1990). Concentrated in the center of the plant, the accumulated resources have maximum protection from fire, while the outer leaves, which are most susceptible to fire damage, can burn with little overall loss of stored carbohydrates. The timing of inflorescence emergence may also be important in reducing fire damage in reproductive agaves. Most natural lightning strikes that result in fires occur from May–August (Sellers and Hill 1974; Swetnam and Baisan 1996b). By this time, flower stalks are generally taller than the surrounding vegetation in grassland communities and above the fire zone (Slauson, personal observation). Spring fires or fires in denser oak woodland communities where the fire zone reaches into tree canopies could potentially damage emerging inflorescences more severely.

Low fruit set is common in outcrossing, hermaphroditic plants such as agave (Sutherland and Delph 1984). Sutherland (1982) found that mean fruit set per inflorescence in paniculate agaves is consistently around 20% despite hand or open pollination treatments, suggesting that fruit set is primarily resource limited. Slauson (2000) studied fruit and seed set in three different open-pollinated populations of *A. palmeri* in Arizona, and also found fruit set to average around 20% while seed set varied from 26–33%. Fire did not appear to affect reproductive output in this study as no significant differences in fruit and seed set were found between burned and unburned plants, and results (Fig. 3) were very similar to previous reports of unburned plants. The rosette shape and translocation of resources in reproductive agaves appear to be important adaptations to fire that protect stored resources critical for reproduction. The significantly lower seed set at the CF site was observed in both burned and unburned plants, and suggests the cause is most likely a result of pollinator and/or resource availability at the site and not a result of burn treatment.

Periodic fires may be important in promoting germination and establishment events of *A. palmeri* by reducing competition and opening up germination sites, especially in dense grassland/woodland habitats. Germination of *A. palmeri* generally occurs in mid-late summer after monsoon rains have begun. During July 1999 (two months after the fire) approximately four inches of precipitation fell at the MF site, and during establishment of demography plots in burned areas in late July–early August, 16 seedlings were observed. These plants were assumed to be seedlings as they were  $<40 \times$

20 mm in height and diameter, and had no burn damage despite being located near burned plants. A cursory search for seedlings was conducted in several unburned areas adjacent to the burned site, but no seedlings were found.

### CONCLUSIONS

Prescribed natural and human-ignited fires are important ecosystem management tools used to alter community composition and forage conditions, decrease fuel accumulation, and reduce the potential of catastrophic, stand-replacing wildfires. Although historic changes in the southwestern U.S. landscape have been significant due to fire exclusion, the return of fire in the sites studied did not appreciably impact nectar and pollen production, fruit and seed set, or initial mortality of *A. palmeri*. Standing crop results indicated that at least through mid-August in the sites examined, food resources of lesser long-nosed bats were not limited as a result of fire. Habitat preferences and several morphological and physiological adaptations appear to adequately protect the majority of stored resources of *A. palmeri* during fire events, although fuel loads within individual microhabitats of agaves can result in variable fire damage to rosettes. Further study is needed to more clearly understand how fire affects population dynamics and mortality of *A. palmeri* beyond the initial post-fire period.

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## ADULT SEX RATIO OF *ARCEUTHOBIUM GILLII* (VISCACEAE)

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### ABSTRACT

The adult sex ratio of *Arceuthobium gillii* was determined from five populations in southern Arizona and one population in Chihuahua, Mexico. A total of 6154 mistletoe plants were sexed on a total of 38 host trees; 3096 of these were male plants (50.3%) and 3058 were female (49.7%). A chi-square analysis indicated that these numbers were not significantly different from an essentially 1:1 sex ratio. Furthermore, although there was variation between trees (more male or female plants) the sex ratio on individual trees, and for each population, was also essentially 1:1.

Key Words: Chihuahua pine dwarf mistletoe, Chihuahua pine, sex ratio

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are dioecious, parasitic flowering plants that commonly occur on members of the Pinaceae in western North America. In general, the sex ratio (female plants : male plants) of dwarf mistletoes has been reported to be 1:1 (Hawksworth and Wiens 1996; Mathiasen et al. 1998). However, other investigators have reported female-biased sex ratios for several dwarf mistletoes: *Arceuthobium americanum* Engelm. in Canada (Muir 1966), *A. globosum* Hawsw. & Wiens subsp. *globosum* and *A. strictum* Hawsw. & Wiens in Durango, Mexico (Hawksworth and Wiens 1996), *A. pusillum* Peck in Minnesota (Baker et al. 1981), and most notably, *A. tsugense* (Rosendahl) G. N. Jones subsp. *tsugense* and subsp. *mertensianae* Hawsw. & Nickrent from the Pacific Northwest and Alaska (Wiens et al. 1996). The majority of these reports of female-biased sex ratios for dwarf mistletoes were based on small sample sizes (approximately 50–500 total plants). However, the latter study used over 3000 plants from 16 populations distributed from southern Oregon to southeast Alaska and reported a significant female-biased sex ratio for 10 of the populations and for the pooled data from all 16 areas (59% females:41% males).

Because of the female-biased sex ratio reported for *Arceuthobium tsugense* (Wiens et al. 1996), Hawksworth and Wiens (1996) recommended that the sex ratios of other dwarf mistletoes be examined. Therefore, this study was initiated to provide additional information on the adult sex ratios of dwarf mistletoes. *Arceuthobium gillii* Hawsw. & Wiens was chosen for this study because of the strong sexual dimorphism exhibited by this species (Hawksworth and Wiens 1996, see page 147). This strong sexual dimorphism allowed male and female plants to be easily distinguished. Other dwarf mistletoes also exhibit extreme sexual dimorphism and

a study of this characteristic would be a valuable contribution to the systematics of the genus (Hawksworth and Wiens 1996, Mathiasen et al. 1998).

### MATERIALS AND METHODS

The adult sex ratio for *Arceuthobium gillii* was determined for five populations in southern Arizona and for one population in Chihuahua, Mexico (Table 1, Fig. 1). At each of the locations sampled, at least four, severely infected Chihuahua pines (*Pinus chihuahuana* Englem.) were selected, their diameters at breast height (1.3 m above the ground) measured to the nearest 0.5 cm, and a dwarf mistletoe rating (DMR) assigned to each tree using the 6-class system (Hawksworth 1977). For reasons of safety and efficiency sampling was restricted to trees <30 cm in diameter at breast height and a DMR >4.

Selected trees were flagged and after diameters and dwarf mistletoe ratings were recorded, each tree was cut as close to the ground as possible. After each tree was cut, its total height to the nearest 0.1 m, was measured. Live branches that broke from the tree when it was cut were examined for mistletoe plants first. Then each live branch still attached to the tree, starting at the bottom of the crown, was removed and examined for mistletoe plants. The sex of each observed plant on a branch was recorded and the branch discarded well away from the tree so the branch would not be re-sampled. This process was repeated until all the live branches on each tree had been examined. Only plants that could be accurately sexed were tallied. One person examined branches for mistletoe plants and one person recorded data. This was to insure that the person examining mistletoe plants did not know how many males or females had been tallied as sampling proceeded. The same person recorded data until a tree had been completed. Data were not summarized until all the selected trees had been

TABLE 1. POPULATION LOCATIONS, NUMBER OF TREES SAMPLED, MEAN DIAMETERS, MEAN DWARF MISTLETOE RATINGS, MEAN TREE HEIGHTS, NUMBER OF PLANTS SAMPLED, AND ADULT SEX RATIOS (PERCENT FEMALE) FOR *ARCEUTHOBium GILLII*. No sex ratios exhibited a significant sex bias. Chi-square statistics ( $P \leq 0.05$ ). DBH = diameter breast height; DMR = dwarf mistletoe rating (Hawksworth 1977).

Population location	Trees sampled	Mean DBH (cm)	Mean DMR	Mean height (m)	Plants sampled	Percent female	P
Bear Canyon Santa Catalina Mountains, AZ	7	16.0	5.3	8.5	1094	47.9	0.164
Gardner Canyon Santa Rita Mountains, AZ	4	15.0	5.3	7.0	511	50.5	0.825
Carr Canyon Huachuca Mountains, AZ	9	16.0	5.6	8.1	1348	50.6	0.663
Pinery Canyon Chiricahua Mountains, AZ	4	18.0	5.6	8.3	1936	50.7	0.525
Upper Cave Creek Chiricahua Mountains, AZ	7	20.0	5.6	10.6	568	49.3	0.737
Chihuahua, Mexico (Sierra Madre Occidental)	7	16.0	5.3	7.2	697	48.2	0.344
Total/mean	38	17.0	5.4	8.4	6154	49.7	0.702

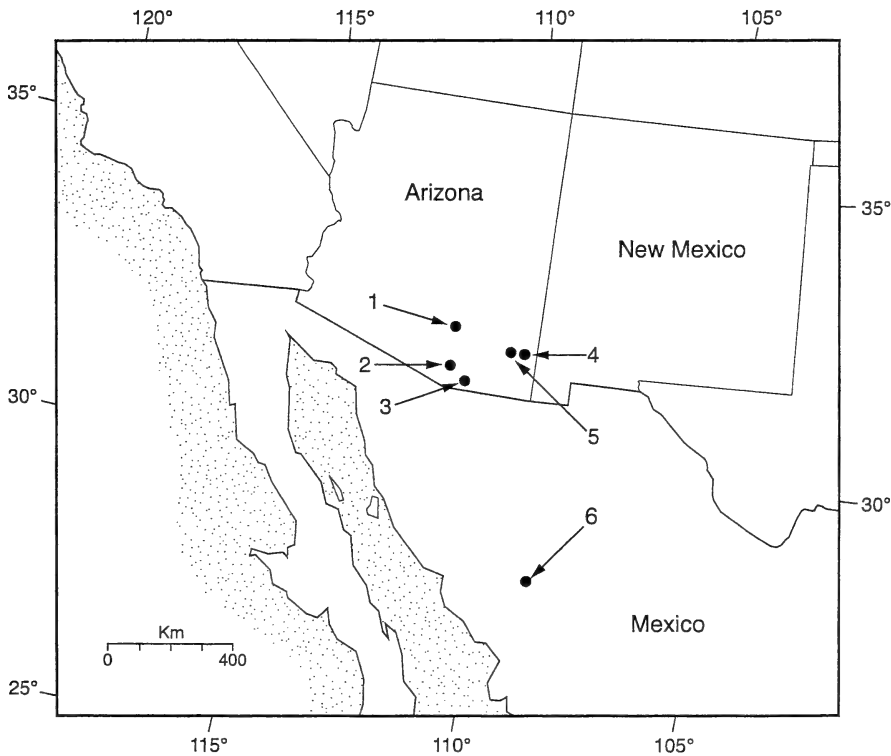


FIG. 1. Approximate locations of study sites. 1—Bear Canyon, Santa Catalina Mountains, Arizona; 2—Gardner Canyon, Santa Rita Mountains, Arizona; 3—Carr Canyon, Huachuca Mountains, Arizona; 4—Pinery Canyon, Chiricahua Mountains, Arizona; 5—Upper Cave Creek, Chiricahua Mountains, Arizona; and 6—Sierra Madre Occidental, Chihuahua, Mexico.

TABLE 2. ADULT SEX RATIOS (PERCENT FEMALE) FOR *ARCEUTHOBium gillii* FOR EACH TREE SAMPLED IN CARR CANYON, HUACHUCA MOUNTAINS, ARIZONA. No sex ratios exhibited a significant sex bias. Chi-square statistics ( $P \leq 0.05$ ). DBH = diameter breast height; DMR = dwarf mistletoe rating (Hawksworth 1977).

Tree number	DBH (cm)	DMR	Height (m)	Plants sampled	Percent female	P
1	16.0	5	8.1	93	54.8	0.351
2	10.5	6	5.6	153	53.6	0.374
3	19.5	6	10.3	196	49.0	0.775
4	16.0	5	7.8	76	44.7	0.359
5	18.0	5	8.7	141	53.2	0.449
6	14.0	6	7.3	83	48.2	0.742
7	20.5	6	8.6	268	49.3	0.807
8	16.5	6	8.1	164	47.6	0.532
9	16.0	5	8.0	174	54.0	0.289
Total/mean	16.0	5.6	8.1	1348	50.6	0.663

sampling. After summarizing the total number of plants sexed for the selected trees, additional trees were sampled to bring the total number of plants sexed to a minimum of 500, if necessary.

Data were collected in May of 1998–2000 and in June 2001. This was either during anthesis of male plants or shortly after it (June). A chi-square analysis was used to determine if the ratio of male to female mistletoe plants exhibited a sex bias. We used a P value of  $\leq 0.05$  to determine the existence of statistically significant differences (Zar 1999).

RESULTS

The general location of study sites, the number of trees sampled, tree mean diameters, mean dwarf mistletoe ratings, mean heights, the number of mistletoe plants sexed, and the percentage of female plants for each population sampled are presented in Table 1. We sampled a total of 6154 mistletoe plants that could be accurately sexed on 38 trees. Of the plants we sexed, 3096 (50.3%) were males and 3058 (49.7%) were females. The difference in the number of male and female plants was not significantly different from the number expected for a 1:1 sex ratio ( $P = 0.628$ ); therefore, the adult sex ratio of *Arceuthobium gillii* on the 38 trees was essentially 1:1 (Table 1).

There was a large amount of variation in the sex ratio for *A. gillii* between individual trees at each of the study sites. An example of this variation is illustrated by the trees sampled in the Huachuca

(Table 2) and Santa Rita Mountains, Arizona (Table 3). Some trees had more female plants than males and vice versa, but no trees exhibited significantly different sex ratios from a 1:1 ratio. In addition, when the sex ratio was determined using all of the trees in each population, no significant differences from a 1:1 sex ratio were detected for any of the populations (Tables 1–3).

DISCUSSION

Although several investigators have reported significant female-biased adult sex ratios for several dwarf mistletoes, we found that the adult sex ratio for *Arceuthobium gillii* is essentially 1:1. These results were expected because many other dwarf mistletoes also have 1:1 adult sex ratios (Hawksworth and Wiens 1996; Mathiasen et al. 1998). Because many of the reports of female-biased adult sex ratios for dwarf mistletoes are based on relatively small sample sizes (<500 plants), they may not represent an accurate estimate of the sex ratios for these mistletoes (Mathiasen and Shaw 1998; Daugherty and Mathiasen 1999).

Our results demonstrate the variation in sex ratio that can occur among individual trees. This tree-to-tree variation has been demonstrated in other studies of mistletoe sex ratio (Nixon and Todzia 1985; Mathiasen and Shaw 1998; Daugherty and Mathiasen 1999). Because of this tree-to-tree variation, a large sample of mistletoe plants should be sampled for dioecious mistletoe sex ratio studies and data

TABLE 3. ADULT SEX RATIOS (PERCENT FEMALE) FOR *ARCEUTHOBium gillii* FOR EACH TREE SAMPLED IN GARDNER CANYON, SANTA RITA MOUNTAINS, ARIZONA. No sex ratios exhibited a significant sex bias. Chi-square statistics ( $P \leq 0.05$ ). DBH = diameter breast height; DMR = dwarf mistletoe rating (Hawksworth 1977).

Tree number	DBH (cm)	DMR	Height (m)	Plants sampled	Percent female	P
1	14.5	5	7.1	113	50.5	0.925
2	10.0	6	5.2	123	54.5	0.321
3	20.0	5	7.9	206	49.0	0.781
4	16.0	5	7.8	69	49.3	0.904
Total/mean	15.0	5.3	7.0	511	50.5	0.825



should be analyzed using the results for the entire population and not on an individual tree basis (Mathiasen and Shaw 1998). We sampled over 6000 adult plants from several separate populations of *A. gillii* and found that this species exhibits a 1:1 adult sex ratio in each population sampled and when the data were pooled for all populations. Therefore, we contend that *A. gillii* will exhibit a consistent 1:1 adult sex ratio whenever large numbers of plants (>500) are sexed for populations of this dwarf mistletoe.

We plan to determine the adult sex ratios for other dwarf mistletoes in the Southwest and for those already reported to have female-biased sex ratios based on small samples, such as *Arceuthobium americanum*, *A. globosum*, and *A. strictum* (Hawksworth and Wiens 1996). However, we now hypothesize that when a large number of dwarf mistletoe plants are sampled for each of these dwarf mistletoes, the overall adult sex ratio will be essentially 1:1 as it was for the populations of *A. gillii* we sampled in this study.

#### ACKNOWLEDGMENTS

We would like to extend our appreciation to Del Wiens for suggesting this study be conducted. The field assistance of Dave Russell in the Chiricahua Mountains is sincerely appreciated also.

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## ANNOUNCEMENT

### FIRST ANNOUNCEMENT AND CALL FOR SESSIONS

### FOURTH INTERNATIONAL SYMPOSIUM ON GRASS SYSTEMATICS AND EVOLUTION AND

### THIRD INTERNATIONAL CONFERENCE ON THE COMPARATIVE BIOLOGY OF THE MONOCOTYLEDONS

The Third International Conference on the Comparative Biology of the Monocotyledons and Fourth International Symposium on Grass Systematics and Evolution will be hosted by Rancho Santa Ana Botanic Garden (Claremont, CA, USA) on 30 March–5 April 2003. Topics will include morphology, anatomy, development, reproductive biology, molecular biology, cytology, genomics, genetics, biochemistry, paleobotany, phylogenetics, classification, biogeography, ecology, and data integration. Sessions will be devoted to particular groups within

monocots such as grasses and orchids. Monocots III will provide a rare opportunity for researchers in diverse fields to interact, share ideas, and form collaborations. We invite proposals from those who wish to organize sessions. A call for contributed papers and posters will follow. The conference proceedings will be published. Springtime marks the flowering peak of the diverse California flora, and field trips are planned. Visit [www.monocots3.org](http://www.monocots3.org) for conference details; or write Monocots III, Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, CA 91711-3157 USA; E-mail [info@monocots3.org](mailto:info@monocots3.org); fax 1.909.626.7670; telephone 1.909.625.8767 ext. 333. Co-sponsors include the American Society of Plant Taxonomists, Botanical Society of America, and the International Association for Plant Taxonomy.

*ERIOGONUM OVALIFOLIUM* VAR. *MONARCHENSE* (POLYGONACEAE),  
A NEW VARIETY FROM THE SOUTHERN SIERRA NEVADA,  
CALIFORNIA

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ABSTRACT

*Eriogonum ovalifolium* var. *monarchense* is a new variety discovered on a limestone formation in the southern Sierra Nevada. It is only known from one population in the Kings River drainage basin. It is morphologically similar to *E. ovalifolium* var. *vineum*; an endangered species found on limestone outcrops in the San Bernardino Mountains. The habit of the two varieties is different primarily in the angle that the flowering stems arise from the base.

Key words: *Eriogonum ovalifolium* var. *monarchense*, Kings River, Sierra Nevada, Monarch buckwheat, limestone

In 1995, botanical explorations in the Kings River canyon of the southern Sierra Nevada yielded three previously unknown vascular plant taxa from the limestone (marble) outcrops around Boyden Cavern, near Kings Canyon National Park. *Heterotheca monarchensis* Semple, Shevock, & York and *Gilia yorkii* Shevock & A. G. Day were described within a few years of their discovery. A new variety of buckwheat from the Boyden Cavern limestone required years of research and follow-up collecting to verify its taxonomic status. The first collections of the three new taxa were made on the same day (31 July 1995) in Monarch Wilderness (Sierra and Sequoia National Forests).

***Eriogonum ovalifolium* Nutt. var. *monarchense***

D. A. York, var. nov. (Fig. 1)—Type: USA, CA, Fresno Co, 86 km E of Fresno, Sierra National Forest, Monarch Wilderness, 2.4 km NW of Boyden Cave on N side of the Kings River canyon, 36°50'08"N, 118°49'19"W (NAD 83), 1815 m, 31 July 1995, York 111 & Shevock (holotype CAS; isotypes JEPS, NY). Paratype: USA, CA, Fresno Co, 86 km E of Fresno, Sierra National Forest, Monarch Wilderness, 2.4 km NW of Boyden Cave on N side of Kings River canyon, 36°50'08"N, 118°49'19"W (NAD 83), 1815 m, 19 July 1996, York 1250 (RSA).

*Eriogonum ovalifolium* var. *vineum* accedentes sed caules floriferentes decumbenti ad ascendenti sunt.

Pulvinate perennials forming mats up to 30 cm across (Fig. 1A); leaves basal, petiolate, tomentose, 5–22 mm long, the margins flat to slightly crisped, petioles 2–10 mm long, blades elliptic to orbicular, 3–12 mm long, 3–12 mm wide; flowering stems scapose, 1—many per matted clump, decumbent to ascending, 2–6(9) cm long, tomentose to floccose;

inflorescences capitate, the head 1.5–4 cm across; bracts scale-like, 3, 1–5 mm long; involucre clustered 4–6 per head, sessile, tomentose, turbinate, 5–8 mm long, with 5 rounded or acute teeth up to 2 mm long; flowers white to cream with green (aging red) midribs, 4–6 mm long, glabrous, the perianth lobes dimorphic, the perianth lobes of the outer whorl mostly twice the width of the inner whorl (Fig. 1B); stamens mostly exserted, 1–3 mm long, the anthers 0.4–0.6 mm long; achenes brown, 2–3 mm long, glabrous.

DISTRIBUTION, HABITAT, AND PHENOLOGY

*Eriogonum ovalifolium* var. *monarchense* (Monarch buckwheat) is a rare neoendemic found in eastern Fresno County, in the southern Sierra Nevada. The only known population (type locality) grows on the north side of a limestone formation in the Kings River canyon above 1800 m (5900 feet), in the vicinity of Boyden Cavern. The plants are located in Monarch Wilderness, just below the Monarch Divide, in the Sierra National Forest. Monarch Divide rises over 880 m above the canyon floor and is the boundary between the middle and south forks of the Kings River and the Sierra and Sequoia National Forests. The divide is rugged and varied with a mix of metamorphic and igneous rocks. The limestone component is typified by steep slopes and sheer cliffs.

*Eriogonum ovalifolium* var. *monarchense* forms dense mats on ledges and crevices in sandy soils developed from decomposed limestone. The population consists of approximately 30 plants scattered over a few thousand square meters. Flowers are present from June to August. Associates include *Argyrochosma jonesii* (Maxon) Windham, *Bromus madritensis* L. ssp. *rubens* (L.) Husn., *Cercocarpus intricatus* Wats., *Erigeron aequifolius* Hall, *Erysimum capitatum* (Dougl.) Greene ssp. *capitatum*, *Garrya flavescens* Wats., *Gilia yorkii*, *Heuchera rubescens* Torr. var. *rydbergiana* Rosend., Butt. &

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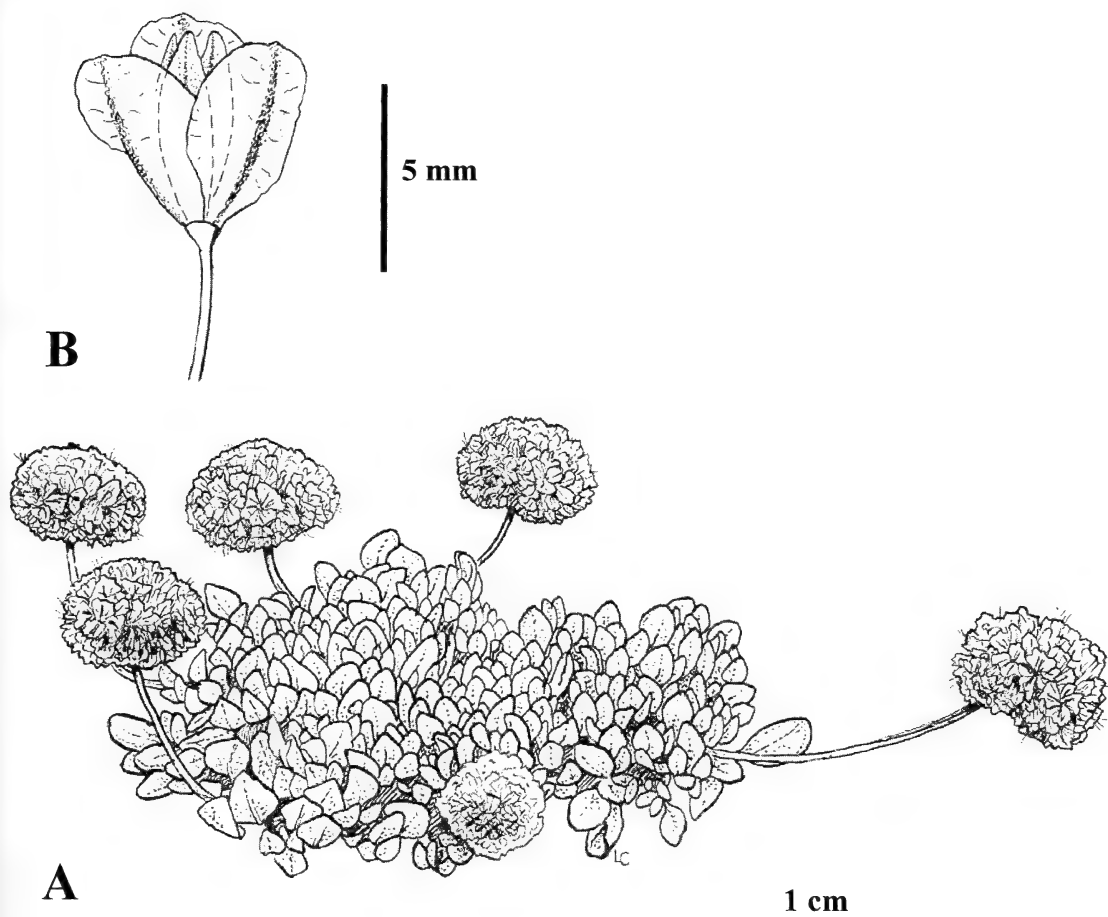


FIG. 1. Habit of *Eriogonum ovalifolium* Nutt. var. *monarchense* D. A. York, and a detailed illustration of a flower from holotype collection and photographs. A. Mature plant in flower. B. Flower with detail of perianth lobes in an erect position. Drawings by Laura Cunningham.

Lak., *Pinus monophylla* Torr. & Frém., *Selaginella asprella* Maxon, *Streptanthus fenestratus* (Greene) J.T. Howell, and *Yucca whipplei* Torr.

#### RELATIONSHIPS

The new taxon differs in several respects from the other California varieties of *Eriogonum ovalifolium* (Table 1). *Eriogonum ovalifolium* var. *monarchense* is morphologically similar to *E. ovalifolium* Nutt. var. *vineum* (Small) Jepson; an endangered species known only from limestone outcrops in the San Bernardino Mountains. *Eriogonum ovalifolium* var. *vineum* has flowering stems that are generally erect in contrast to the decumbent to ascending flowering stems of *E. ovalifolium* var. *monarchense*. These two varieties occur in disjunct mountain ranges and are approximately 325 km apart from each other.

*Eriogonum ovalifolium* Nutt. var. *purpureum* (A. Nelson) Durand is a variety that occurs in the east-

ern Sierra Nevada and other mountain ranges in western North America on various substrates (Reveal 1989). It differs from *E. ovalifolium* var. *monarchense* by having longer leaf blades and shorter involucre.

*Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) M.E. Jones is geographically close to, but not sympatric with, *E. ovalifolium* var. *monarchense*. In California, it occurs mostly on granites in subalpine and alpine habitats throughout the Sierra Nevada, Cascades, and White Mountains (Hickman 1993). It differs from *E. ovalifolium* var. *monarchense* by having generally smaller leaves and shorter flowering stems and perianth lobes.

#### KEY TO THE CALIFORNIA VARIETIES OF *ERIOGONUM OVALIFOLIUM*

- 1a. Flowers yellow ..... var. *ovalifolium*
- 1b. Flowers white, cream, red, or purplish
  - 2a. Flowers 2–3 mm long ..... var. *nivale*

TABLE 1. COMPARISON OF *ERIOGONUM OVALIFOLIUM* VAR. *MONARCHENSE* WITH THE OTHER *E. OVALIFOLIUM* VARIETIES KNOWN FROM CALIFORNIA.

Characters	<i>E. o. monarchense</i>	<i>E. o. eximium</i>	<i>E. o. nivale</i>	<i>E. o. ovalifolium</i>	<i>E. o. purpureum</i>	<i>E. o. vineum</i>
Flowering stems	decumbent to ascending	erect	erect	erect	erect	erect
Leaf blades	2-5 cm long unmargined elliptic to orbicular	5-10 cm long brown-margined elliptic to spatulate	0.3-5 cm long ± unmarginated orbicular	4-20 cm long ± unmarginated obovate	5-20 cm long ± unmarginated obovate	3-6 cm long unmarginated orbicular
Involucre lengths	0.3-1.2 cm long	0.5-2 cm long	0.2-0.8 cm long	1-6 cm long	0.5-2 cm long	0.6-1.2 cm long
Flowers	5-8 mm white to cream	4-6.5 mm white to cream	2-4 mm white to cream	4-6.5 mm yellow	4-6.5 mm purple or white to cream	5-7 mm white to cream
Habitat	4-6 mm long rocky limestone	4-6 mm long sandy granites	2-3 mm long sandy or gravelly granites	4-6 mm long sandy or gravelly various substrates	4-6 mm long sandy or gravelly various substrates	3-5 mm long rocky limestone
Range	S. Sierra Nevada, California 1800 m elev.	N. Sierra Nevada, Nevada 1800-3400 m elev.	W. North America 1500-4100 m elev.	W. North America 1200-2900 m elev.	W. North America 1200-2800 m elev.	San Bernardino Mtns. 1500-2100 m elev.

- 2b. Flowers >3 mm long
- 3a. Leaves obviously brown-margined . . . . . var. *eximium*
- 3b. Leaves not distinctly brown-margined
- 4a. Flowering stems 4-20 mm long; involucre 4-6.5 mm long; various substrates . . . . . var. *purpureum*
- 4b. Flowering stems 2-6 (9) mm long; involucre 5-8 mm long; carbonate substrates
- 5a. Flowering stems decumbent to ascending; southern Sierra Nevada Range . . . var. *monarchense*
- 5b. Flowering stems mostly erect; San Bernardino Mountains . . . . . var. *vineum*

DISCUSSION

*Eriogonum ovalifolium* var. *monarchense* is allopatric from the other varieties of *E. ovalifolium*. The calcareous habitat and associated species where *Eriogonum ovalifolium* var. *monarchense* is found are more typical of pinyon pine communities in the eastern Sierra Nevada and the desert ranges of California and Nevada. It is possible that *Eriogonum ovalifolium* var. *monarchense* is allied with the varieties from the desert and southern California mountains and not with the Sierran *Eriogonum ovalifolium* var. *nivale*. There are four other calcicole vascular plants endemic to the King River basin (York 1999). These include *Eriogonum nudum* Benth. var. *regirivum* Reveal & J. Stebbins, *Gilia yorkii*, *Heterotheca monarchensis*, and *Streptanthus fenestratus*. *Heterotheca monarchensis* (occurs on south-facing slopes with a population very near *Eriogonum ovalifolium* var. *monarchense*) and *Gilia yorkii* are allied with their respective desert congeners (York 1999). They evolved from desert taxa that spread into the California Floristic Province during Xerothermic periods of the Quaternary (York 1999). Other evidence of this desert link include taxa found on the limestone outcrops around Boyden Cavern, such as *Achnatherum hymenoides* (Roem. & Schultes) Barkworth, *Argyrochosma jonesii*, *Melica frutescens* Scribn., and *Petrophyton caespitosum* (Nutt.) Rydb., that are mostly rare in the Sierra Nevada and common in the desert ranges (York 1999).

RARITY

*Eriogonum ovalifolium* var. *monarchense*, previously unknown and uncollected, is a rare taxon due to its lithophytic nature on limestone, a relatively uncommon substrate in the southern Sierra Nevada. Because of the remoteness and rugged physiography of the Kings River canyon limestones, it is unlikely that *Eriogonum ovalifolium* var. *monarchense* occurs outside the river basin. It is a rare and localized endemic worthy of conservation efforts. Anthropogenic impacts are not likely because the population is remote and within a designated wilderness. If the type

locality is indeed the only population, then this taxon is vulnerable to extinction due to stochastic events or genetic drift.

ACKNOWLEDGMENTS

I thank Laura Cunningham for her carefully detailed work on the illustrations, and Johanna Arnegger (my Austrian friend) for correcting the Latin diagnosis. I also thank Jim Shevock for following me through poison oak, dense brush, loose rock, and up steep slopes during an uncomfortably hot day to assist me in collecting the type mate-

rial. James Reveal and an anonymous reviewer provided useful comments on my drafts for which I am grateful.

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*HESPEROYUCCA WHIPPLEI* AND *YUCCA WHIPPLEI* (AGAVACEAE)

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ABSTRACT

The name *Yucca whipplei* dates from 1861, not 1859. The names *Hesperoyucca*, *Hesperoyucca whipplei*, and *Hesperoyucca whipplei* var. *graminifolia* date from 1893.

Chaparral yucca has been widely known for 140 years or so as *Yucca whipplei*. The plants have long been recognized as markedly unlike other yuccas (e.g., Engelmann 1871). Baker (1892) suggested the plants are generically distinct from other yuccas. But, chaparral yucca has continued to reside within *Yucca* in most taxonomic and floristic treatments. Primarily on molecular similarities and differences, Bogler and Simpson (1995), Clary and Simpson (1995), and others cited by them, have revived the suggestion that chaparral yucca should be placed in a separate genus, *Hesperoyucca*. Here, we review the histories of the botanical names.

When the name *Yucca whipplei* was first used in print, Torrey (1859, p. 222) described (or at least diagnosed) the taxon and wrote, "If it prove to be a distinct species it may be called *Y. Whipplei*." We consider that use of *Yucca whipplei* by Torrey to have been as a provisional name and, therefore, we believe that the name was not validly published in 1859. The next use of *Yucca whipplei* that we have found was also by Torrey (1861). Conditions for valid publication of *Yucca whipplei* were met by Torrey in 1861. We believe the correct citation to be:

***Yucca whipplei*** Torrey in J. C. Ives, Rep. Colorado R. 4(Botany):29. 1861.

Plants of *Yucca whipplei* have also been called *Hesperoyucca whipplei*. There is no entry for *Hesperoyucca* in the published version of ING (Farr et al. 1979). In June 2001, requests to the website for Index Nominum Genericorum (currently, <http://rathbun.si.edu/botany/ing/>) for *Hesperoyucca* elicited the response, "No records found with: Search for Name '*Hesperoyucca*.'"

The earliest use of *Hesperoyucca* of which we are aware was by Engelmann (1871), who partitioned *Yucca* into: "§ EU-YUCCA," with three subordinate groups (*Sarcocarpa*, *Clistocarpa*, and *Chaenocarpa*) with one species each, and "§ HESPERO-YUCCA," which included *Yucca whipplei*

as the only species. In 1873, Engelmann provided a summary "SYSTEMATIC ARRANGEMENT" for *Yucca* in which he named: I. Euyucca (which included: A. *Sarcocarpa*, B. *Clistocarpa*, and C. *Chaenocarpa*) and II. *Hesperoyucca*. In both classifications, the rankless *Hesperoyucca* included only *Yucca whipplei*.

In a third paper ("corrections and additions" to the 1873 paper), Engelmann (1875) provided yet another "synopsis" for *Yucca* and that time partitioned *Yucca* into four coordinate elements named *Sarcocarpa*, *Clistocarpa*, *Chaenocarpa*, and *Hesperoyucca*. Once again, Engelmann did not indicate rank for his subdivisions of *Yucca*.

Baker (1876), in notes on *Yucca whipplei*, wrote, "... Dr. Engelmann, who has considered it [i.e., *Yucca whipplei*] as the type of a new subgenus, which, alluding to its western locality, he has called *Hesperoyucca*. At present this subgenus is only known to contain a single species." We believe that Baker's remarks were sufficient to establish subgeneric rank and that the correct citation is:

***Yucca* L. subg. *Hesperoyucca*** (Engelmann) Baker, Gard. Chron. n.s. 6:196. 1876. Based on *Yucca* [unranked] *Hesperoyucca* Engelmann in S. Watson et al., Botany (Fortieth Parallel), 497. 1871, as "§ 2. HESPERO-YUCCA."

In 1892, Baker wrote of *Y. whipplei*, "I now think this had better be kept as a genus distinct from *Yucca*, under Engelmann's name *Hesperoyucca*." Baker, nevertheless, treated *whipplei* as belonging to *Yucca* in 1892. We suggest that Baker's statement in 1892 may have been a "note-added-in-proof" and that Baker's statement was not sufficient to establish generic rank for *Hesperoyucca*.

Trelease (1893) accepted Baker's suggestion of generic rank for *Hesperoyucca*, made a specific combination in *Hesperoyucca*, and coined a varietal nomen novum in *Hesperoyucca*. We believe correct citations for the names are:

**Hesperoyucca** (Engelmann) Trelease, Rep. (Annual) Missouri Bot. Gard. 4:208. 1893. Based on: *Yucca* [unranked] *Hesperoyucca* Engelmann in S. Watson et al., Botany (Fortieth Parallel) 497. 1871. —Type: *Hesperoyucca whipplei* (Torrey) Trelease = *Yucca whipplei* Torrey.

**Hesperoyucca whipplei** (Torrey) Trelease, Rep. (Annual) Missouri Bot. Gard. 4:208. 1893, as '*Y. Whipplei*' under 'HESPEROYUCCA'. Given the use of *Hesperoyucca whipplei* elsewhere in the article by Trelease (figure captions, in a name at varietal rank), we consider the "Y" at the comb. nov. to be a typographic error and the attribution of the combination to Baker to have been superfluous. Basionym: *Yucca whipplei* Torrey.

**Hesperoyucca whipplei** (Torrey) Trelease var. **graminifolia** Trelease, Rep. (Annual) Missouri Bot. Gard. 4:215. 1893. We maintain that Trelease coined a nom. nov. based on: *Yucca graminifolia* Wood, 1868 [Proc. Acad. Nat. Sci. Philadelphia 20:167], non Zucc., 1837.

After submitting this paper to Madroño for publication (June 2001), drafts of the manuscript (or relevant excerpts) were sent to colleagues with especial interest in botanical nomenclature. A flurry of e-mails ensued. Some nomenclaturists held that Baker validated *Hesperoyucca* at generic rank in 1892. Others opined that Baker did not validly publish *Hesperoyucca* at generic rank and that *Hesperoyucca* was validly published at generic rank by Trelease in 1893. To us, Baker explicitly treated *Hesperoyucca* at subgeneric rank in 1876 and did not explicitly treat *Hesperoyucca* at generic rank in 1892.

As a result of having the matter of valid publication of *Hesperoyucca* at generic rank bandied about, the website for ING posted this entry in November 2001:

**Hesperoyucca** (G. Engelmann) J. G. Baker, Bull. Misc. Inform. Kew 1892: 8. Jan 1892.

T.: *H. whipplei* (J. Torrey) W. Trelease ('*Y. whipplei*') (Rep. (Annual) Missouri Bot. Gard. 4: 208. 1893) (*Yucca whipplei* J. Torrey)

*Yucca* [unranked] *Hesperoyucca* G. Engelmann in S. Watson, U.S. Geol. Surv. 40th Parallel, Bot. 497. Sep–Dec 1871.

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In December 2001, after further bandying, the ING website entry was changed to:

**Hesperoyucca** (G. Engelmann) W. Trelease, Rep. (Annual) Missouri Bot. Gard. 4: 208. 9 Mar 1893.

T.: *H. whipplei* (J. Torrey) W. Trelease ('*Y. whipplei*') (*Yucca whipplei* J. Torrey)

*Yucca* [unranked] *Hesperoyucca* G. Engelmann in S. Watson, U.S. Geol. Surv. 40th Parallel, Bot. 497. Sep–Dec 1871. For the publication date, see l.c. (Rep.) 5: 3. 1894.

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SYMPATRY BETWEEN DESERT MALLOW, *EREMALCHE EXILIS* AND  
KERN MALLOW, *E. KERNENSIS* (MALVACEAE): MOLECULAR  
AND MORPHOLOGICAL PERSPECTIVES

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ABSTRACT

Molecular and morphological data support an extended distribution of *Eremalche exilis* into the southern San Joaquin Valley and southern Inner South Coast Ranges of California, within the range of the morphologically similar, rare, and endangered *E. kernensis*. Nuclear rDNA sequences for plants from Kern County that were morphologically indistinguishable from *E. exilis* were identical at all non-poly-morphic sites to sequences of undisputed *E. exilis* from the Mojave Desert and Sonoran Desert, but differed from sequences of *E. kernensis* by seven sequence mutations. Morphologically, *E. exilis* can be distinguished from *E. kernensis* by anther position—in flowers of *E. exilis*, the anthers are held at the same level as the stigmas; in bisexual flowers of *E. kernensis*, the anthers are situated well below the stigmas. Based on limited rDNA data, we found no evidence of gene flow between sympatric populations of *E. exilis* and *E. kernensis*.

Key words: *Eremalche*, Malvaceae, California floristics, ITS, ETS, rare and endangered plants.

Botanists have disagreed about whether the desert mallow, *Eremalche exilis* (A. Gray) Greene, occurs within the California Floristic Province (Kearney 1956; Twisselmann 1956, 1967; Hoover 1970; Bates 1992). In *The Jepson Manual*, Bates (1993) indicated that the distribution of *E. exilis* in California is restricted to the Mojave and Sonoran Deserts, whereas Twisselmann (1956, 1967) and Hoover (1970) indicated that *E. exilis* occurs in the San Joaquin Valley and Inner South Coast Ranges of western Kern County and eastern San Luis Obispo County, California. If *E. exilis* is present in the southern San Joaquin Valley and southern Inner South Coast Ranges of California, then it may be of importance for evaluating the origin and status of the rare and endangered Kern mallow, *E. kernensis* C. B. Wolfe [= *E. parryi* subsp. *kernensis* (C. B. Wolfe) D. M. Bates pro parte; Bates (1992) expanded the circumscription of Kern mallow], which is endemic to the region. *Eremalche kernensis* has been suggested to be of hybrid origin between *E. exilis* and the widespread central Californian taxon *E. parryi* (Greene) Greene (Kearney 1956). A co-occurrence of these taxa would be relevant to that hypothesis. Here we present molecular and morphological data that support an extended distribu-

tion of *E. exilis* into the southern San Joaquin Valley and southern Inner South Coast Ranges of California, within the range of *E. kernensis*.

MOLECULAR DATA

Plants from Kern County that we could not distinguish morphologically from *E. exilis* were included in an ongoing project that aims to clarify whether *E. kernensis* is evolutionarily distinct from *E. parryi* (i.e., that the two taxa are independent, non-interbreeding, evolutionary lineages). Individuals from two populations of putative *E. exilis* from western Kern County were sampled for the molecular analysis. One specimen (Cypher 99-1A) was collected in the Lokern Natural Area (T29S, R22E, sect. 29 SE¼ of NW¼ of SE¼, MDM), and was growing intermixed with the rare and endangered Kern mallow, *E. kernensis*. The other specimen (Vanherweg 99-14) was collected on a hillside west of Derby Acres (T31S, R22E, sect. 10 E½ of NW¼, MDM). In addition, one sample of *E. exilis* from the Mojave Desert (Heckard 4508) as well as several samples of *E. kernensis* were included. The DNA was extracted from pressed and dried leaf material of individual plants and the Internal and 3'-External Transcribed Spacers (ITS and ETS) in



TABLE 1 VARIABLE NUCLEOTIDE POSITIONS IN THE INTERNAL (ITS) AND EXTERNAL (ETS) TRANSCRIBED SPACER REGIONS OF *E. EXILIS* AND *E. KERNENSIS*. Vouchers are deposited at JEPS and sequences at EMBL. *EC* = *E. Cypher*; *BV* = *B. Vanherweg*; *SB* = San Bernardino Co.; \* = non-identical nucleotide positions between *E. exilis* and *E. kernensis*; Each number corresponds to one DNA position and polymorphic positions are abbreviated: s = cg; y = ct; w = at; k = gt; r = ag; m = ac. ? = not sequenced. – = gap; NN = ac/–.

Taxon	Collection data	Accession numbers	ITS (1–646) and ETS (710–1152) positions
ITS/ETS			* * * * *
			11111111222444667778889999900001111
			01124457236789041131221377901261335
			91205885908487260955567839462153782
<i>E. exilis</i>	Kern <i>EC</i> 99-1A	AJ416060/AJ416065	cgctcctcagctacgcgcgggctgtccttccttaacs
<i>E. exilis</i>	Kern <i>BV</i> 99-14	AJ416062/AJ416067	cgctcctcagctacgcg?gggctgtccttycwtacs
<i>E. exilis</i>	SB <i>Heckard</i> 4508	AJ416061/AJ416066	catcctyagctacgmgmkrcrtctmtyctyaag
<i>E. kernensis</i>	Kern <i>EC</i> 99-3	AJ416063/AJ416064	ygyyyyycmrmcryrc?ngg--gctcwgcgctNNg

the nuclear ribosomal DNA were amplified and sequenced as described by Andreasen and Baldwin (2001).

ITS and ETS sequences for plants identified on the basis of morphology as *E. exilis* from western Kern County were identical to the ITS and ETS sequences for undisputed *E. exilis* from the Mojave Desert, except at twelve nucleotide positions (Table 1). At eleven of these positions one or two of the *E. exilis* samples were polymorphic, with one additional nucleotide besides the one present in the non-polymorphic sample(s). At one position, *E. exilis* from the Mojave Desert had a unique state (position 111). ETS and ITS sequences of *Eremalche kernensis* (one sample sequence is shown in Table 1) were polymorphic for many positions but not for the same positions that were polymorphic in the samples of *E. exilis*. In addition to the polymorphic positions, *E. exilis* samples and *E. kernensis* differed at eight nucleotide positions in the ETS and ITS sequences. In the ITS region, the two taxa differed by two point mutations (positions 268 and 646). In the ETS, *E. exilis* and *E. kernensis* differed by four point mutations (positions 938, 973, 1006, and 1021) and *E. exilis* was marked by a two base pair insertion (at positions 825 and 826). This insertion was unique for *E. exilis* and was not present in *E. rotundifolia* or any other sequenced taxon from tribe Malveae (Andreasen and Baldwin 2001, unpublished data). In addition, ETS sequences of *E. kernensis* were polymorphic for a two base-pair indel (ac/–; NN in Table 1) at positions 1137 and 1138. All other Malveae sequences had “ac” at these positions. Phylogenetic analysis of ETS and ITS sequences for each of the taxa of *Eremalche* and various outgroup taxa in tribe Malveae affirmed that samples of *E. exilis* from the Mojave Desert and western Kern County constitute a lineage (data not shown).

MORPHOLOGICAL AND DISTRIBUTIONAL DATA

Overlapping variation in flower color, flower size, and growth form has contributed to uncertain-

ty about the identity of *Eremalche* populations in the southern San Joaquin Valley and southern Inner South Coast Ranges. Both *E. exilis* and *E. kernensis* most commonly have white petals, although petals of *E. exilis* may be tinged with pink and petals of *E. kernensis* occasionally are pale lavender (Wolf 1938; Kearney 1956; Cypher unpublished data). Keys to species of *Eremalche* typically have used petal and calyx lengths to distinguish *E. exilis* from *E. kernensis* and *E. parryi* (e.g., Kearney 1956; Munz 1968; Bates 1993). However, these keys failed to differentiate petal length by gender. *Eremalche exilis* has only bisexual flowers, whereas *E. kernensis* is gynodioecious, i.e., with bisexual-flowered plants and pistillate-flowered plants (Bates 1992, 1993). In *E. kernensis*, petals of pistillate plants are shorter (3 to 7 mm long) than petals of bisexual plants (4.5 to 10 mm long) (Cypher unpublished data). Pistillate plants of *E. kernensis* have petals that often are similar in size to those of *E. exilis*, which has petals ranging in length from 4 to 5.5 mm (Bates 1993).

For the most part, pistillate flowers of *E. kernensis* have only styles and no stamens, but in a small percentage of flowers, there may be a few (less than five, Cypher unpublished data) vestigial stamens that are reduced in size and do not shed pollen. The absence of stamens (or, more infrequently, the presence of few, vestigial, non-functional stamens) in small-flowered (pistillate) plants of *E. kernensis* should be sufficient to distinguish morphologically *E. kernensis* from *E. exilis*, but the differing position of the anthers relative to the stigmas in the two taxa has caused confusion. In *E. exilis*, the anthers are held at the same level as the stigmas, whereas in bisexual flowers of *E. kernensis* the anthers are situated well below the stigmas, near the base of the corolla. Thus, bisexual flowers of *E. exilis* have been mistaken for pistillate flowers of *E. kernensis*, when anthers at the same level as the stigmas have been interpreted as stigmas. The growth form of *E. exilis* has been described as prostrate or decumbent (Munz 1968; Bates 1993), whereas *Eremalche ker-*

*nensis* stems may be erect or prostrate (Wolf 1938; Munz 1968). We have observed erect, slender-stemmed plants of *E. exilis* in western Kern County, as well as individuals of both *E. exilis* and *E. kernensis* that have a stout, erect central stem and several prostrate lateral stems.

Investigations in the Lokern area of western Kern County (west of the community of Button-willow) from 1996 through 2001 revealed that *E. kernensis* does not range more than 3.2 km south of Lokern Road. The southernmost occurrences of *E. kernensis* that we have confirmed are in T29S, R22E, sect. 27, 28, and 29, MDM. Based on morphological characters, we have confirmed the presence of *E. exilis* in T29S, R22E, sect. 14, 19, 20, 23, 24, 27, 28, 29, 32, and 33, MDM; in T30S, R22E, sect. 4; and in T31S, R22E, sect. 10, MDM. *Eremalche exilis* and *E. kernensis* are sympatric in at least T29S, R22E, sect. 14, 20, 23, 27, 28, and 29, MDM, sometimes growing in mixed colonies.

In addition to the above mentioned localities we have identified four collections (at UC) from the southern Inner South Coast Ranges and southern San Joaquin Valley of California that match the description of *E. exilis*: (1) Hoover 9350, collected in 1965 in San Luis Obispo County ("Hill just east of San Juan River, La Panza District, in sandy calcareous soil"); (2) Hoover 441, collected in 1935 in Fresno County ("10 mi e. of Coalinga"); (3) Alice Eastwood s. n., from "Huron, Calif." in Fresno County (this collection is from 1893, before the Huron vicinity was converted to farmland); and (4) Dean Wm. Taylor 10171, collected in 1989 in Kern County ("just west of California Aqueduct ca. 1.3 miles SE of Highway 58"). The fourth collection (Dean Wm. Taylor 10171) yielded ETS and ITS sequences that were identical to ETS and ITS sequences of one of the *E. exilis* specimens from Kern County described above (Cypher 99-1A) except at ETS position 1152, where DWT 10171 had a "g" and Cypher 99-1A had a "cg."

#### CONCLUSIONS

The morphological and molecular data presented here lead us to suggest that *Eremalche exilis* has a wider distribution in California than the distribution reported in *The Jepson Manual* (Bates 1993). The distribution of *E. exilis* should be extended beyond the Mojave Desert and Sonoran Desert to include the California Floristic Province (southern San Joaquin Valley and Inner South Coast Ranges) in Kern and San Luis Obispo counties. Since there are no known recent collections of *E. exilis* from Fresno County it is uncertain if it still occurs there. The

habitat destruction in the San Joaquin Valley suggests that *E. exilis* is likely to have disappeared from the Huron area. In contrast to the extended distribution of *E. exilis*, the range of the rare and endangered *E. kernensis* may be even narrower than previously believed because of earlier mis-identifications of *E. exilis* as *E. kernensis*.

The molecular data demonstrate that *E. exilis* and *E. kernensis* are genetically and evolutionarily distinct entities. Seven sequence differences between them were found, including one insertion unique for *E. exilis*. These positions are not polymorphic in either taxon, contrary to the expectation for hybridizing taxa. We found no evidence of gene flow between *E. exilis* and *E. kernensis* in rDNA sequences of plants collected from the one area of sympatry sampled in this study. The previously proposed hybrid origin of *E. kernensis* and its genetic distinctness from *E. parryi* is under continuing investigation and will be addressed in a later paper.

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POLLINATION OF *CYTISUS SCOPARIUS* (FABACEAE) AND  
*GENISTA MONSPESSULANA* (FABACEAE), TWO INVASIVE  
SHRUBS IN CALIFORNIA

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ABSTRACT

Mutualistic interactions between natives and non-natives, and between different introduced species, can play an important role in the invasion process. The facilitation of a new introduced species by a previous invader could either accelerate an invasion or exacerbate its impact, providing a positive feedback loop in heavily invaded ecosystems. Open grasslands in Marin County, CA, are being invaded by two closely related, introduced legumes, *Cytisus scoparius* (Scotch broom) and *Genista monspessulana* (French broom). These non-clonal shrubs have been shown to be non-autogamous and pollen limited, underscoring the potential importance of pollinators to their fecundity and spread. The flowers of both are fused shut and require forced “tripping” by a pollinator. We measured floral characters and pollen production to make predictions about which species would be most attractive, and most accessible, to bee visitors. *Cytisus* flowers were an order of magnitude larger and produced four times as many pollen grains, suggesting that they should be more attractive and rewarding than *Genista* flowers. However, *Cytisus* flowers also required significantly more force to open, suggesting that less powerful pollinator species might be excluded from visiting. We tested these predictions by quantifying visitation rates and directly observing pollinators at two sites where the invaders co-occur. Consistent with the mechanical assay, pollinators were more successful at accessing flowers of the small-flowered *Genista* than the large-flowered *Cytisus*; however, *Cytisus* was more frequently visited than *Genista*, suggesting that pollinators preferred the larger and more rewarding species. We did not find evidence to support the prediction that the small-flowered *Genista* was accessible to a greater diversity of pollinator species. Although introduced from the same native range as the two plant invaders, honey bees (*Apis mellifera*) were not “better” pollinators than native bumble bees (*Bombus vosnesenskii*) in terms of effectiveness at tripping flowers or the number of flowers visited per plant. However, *Apis* was the numerically dominant pollinator at both sites, underscoring the potential conservation implications of local *Apis* introduction for the spread of noxious weeds in natural ecosystems.

Key words: exotic, introduced, alien, mutualism, plant-pollinator, invasional meltdown

INTRODUCTION

Biological invasions have become one of our most alarming conservation issues (Williamson 1996; Parker and Reichard 1998; Mooney and Hobbs 2000). Negative interactions such as competition and predation between introduced and native species (“biotic resistance”) have long been thought to play a central role in determining whether an invasion will succeed or fail (Darwin 1865; Elton 1958; Levine 2000; Maron and Vila 2001). However, mutualistic interactions between natives and non-natives may also be important in the invasion process (Simberloff and Von Holle 1999; Richardson et al. 2000). Interactions between dif-

ferent introduced species can be important too, as suggested by the idea of “invasional meltdown” (Simberloff and Von Holle 1999; Parker et al. 1999), where the facilitation of a new introduced species by a previous invader could either accelerate an invasion or exacerbate its impact, providing a positive feedback loop in heavily invaded ecosystems. For example, spread of the nitrogen-fixing tree *Myrica faya* in Hawai’i appears to occur primarily through dispersal by an introduced bird species, *Zosterops japonica* (Vitousek and Walker 1989).

The interaction between plants and their pollinators is an example of a mutualism that can exert strong control over the fitness of the interacting partners and is thought to have driven the evolution of many floral traits (Darwin 1877; van der Pijl 1961). Pollinator limitation of plant reproduction is

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common (Burd 1994) and could be especially important for introduced species. A successful invasive plant must be able to colonize new territory, usually in small numbers, and in the absence of its original pollinators. Such a scenario would appear to favor species that are self-fertile and capable of autonomous self-pollination, or autogamy (Allard 1965; Baker 1965; Brown and Marshall 1981; Barrett 2000).

Open grasslands in Marin County, California, are being invaded by two closely related European shrubs, *Cytisus scoparius* (L.) Link (Scotch broom) and *Genista monspessulana* (L.) L. Johnson (French broom). Both species were first introduced to California as ornamentals in the 1860's and 1870's (Hoshovsky 1986). *Cytisus* and *Genista* are non-clonal legumes, are very similar in appearance, and are often lumped together in discussions of their ecological role as invaders (McClintock 1985; Hoshovsky 1986). Despite the above prediction that successful invaders should be self-fertile and autogamous, in previous work we found that neither of these species showed substantial autogamy when pollinators were excluded, and that both exhibited reduced seed set when fertilized with self pollen (Parker and Haubensak 2002). We also found that both species were significantly pollen limited in populations on the Marin Peninsula (Parker and Haubensak 2002). These results demonstrate that the abundance and behavior of pollinators have important consequences for the reproductive success of both these invaders. At the same time, however, there are apparent differences in floral biology between the two species which we predicted could differentially affect their pollination success. Flowers of *Cytisus* appear larger than those of *Genista*. Reproductive plants of both species vary in size from 0.5 m to >2 m, so although *Genista* produces more of its small flowers for a branch of the same size (Parker and Haubensak, unpublished data), both plants can have from several dozen to several thousand yellow flowers. Therefore the primary difference in floral display that distinguishes the species appears to be flower size. Neither plant produces nectar, so pollen is the only reward for insect visitors.

Theoretical expectations led us to pose two alternative hypotheses about how differences between the two species could influence their reproductive success. The first hypothesis involves the ease of handling of flowers by pollinators. Larger flowers like those of *Cytisus* may be more difficult to handle, preventing the access of certain insect species and leading to specialization on a narrower set of pollinators. Both *Cytisus* and *Genista* have typical papilionaceous legume flowers, but with fused keel petals that an insect visitor must split in order to release the style and anthers. Flower visitors may have to apply more force to trip larger flowers (Westerkamp 1997), which could restrict

the diversity and number of visitors to the larger *Cytisus* flowers.

The second, alternative, hypothesis is that the larger *Cytisus* flowers are more attractive and rewarding than the smaller *Genista* flowers. Pollinators often prefer larger flowers or flowering displays (Campbell 1989; Ohara and Higashi 1994; Schemske and Ågren 1995), or larger rewards such as nectar or pollen (e.g., Neiland and Wilcock 1998; Robertson et al. 1999). Flower size can be correlated with nectar production (Brink and de Wet 1980; Harder and Cruzan 1990; Cresswell and Galen 1991), although little is currently known about how flower size correlates with pollen quantity or quality among related species. A large-flowered species like *Cytisus* should attract more pollinators than an otherwise similar, small-flowered species, especially if it offers larger pollen rewards.

We measured floral characters and pollen production in *Cytisus* and *Genista*. Armed with information on the basic floral biology of the two species, we then tested whether patterns in pollinator visitation, the identity and diversity of visiting insect species, and pollinator behavior were consistent with the first or second hypothesis. The purpose of this study, then, was: 1) to investigate floral traits that may influence attraction, specialization, and pollinator effectiveness; 2) to determine whether visitation rates to these two plant invaders were consistent with predictions based on their floral characters; 3) to determine the identity and origin (native vs. non-native) of insect species pollinating *Cytisus* and *Genista* in central California, and 4) to compare the relative "quality" of pollinators from the introduced range vs. the native range of the invaders.

## METHODS

### Study Sites

We conducted our study at two sites in Marin County, CA. The Mt. Tamalpais site is along the eastern edge of Mount Tamalpais State Park, on an exposed, west-facing slope. This site was dominated by non-native grasses, with patches of *Baccharis pilularis*, *Vinca major*, *Cotoneaster pannosa*, *Plantago lanceolata*, *Rubus laciniatus*, and *Conium maculatum*. *Cytisus* and *Genista* grew interleaved, with *Cytisus* individuals somewhat more sparse and spread out than *Genista*. Overall cover of *Cytisus* and *Genista* at the site was approximately 15% and 30%, respectively.

The China Camp site is located 12 km away from the first site, near China Camp State Park. The site is located in a wide ravine, with mixed evergreen woodland on one side and a steep, NE-facing slope on the other side. *Cytisus* and *Genista* grow in patches and as scattered individuals on the ravine bottom and up the NE-facing slope, with a total cover of approximately 15% and 35%, respectively. Other common species included *Heteromeles ar-*

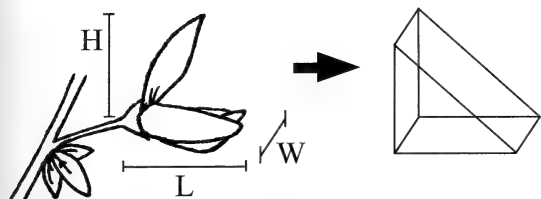


FIG. 1. Schematic to illustrate size measurements conducted on the flowers of *Cytisus* and *Genista*. Flower volume was approximated from a polyhedron using length and width of the keel and height of banner petal.

*butifolia*, *Toxicodendron diversilobum*, *Cortaderia selloana*, *Baccharis pilularis*, *Carduus nutans*, and non-native grasses.

Temperature probes at each site recorded air temperatures at 15 min intervals from April 2 through May 31. The two sites were similar for daily maximum, minimum, and mean temperatures between 9 am and 6 pm. For example, the average daily temperature ( $^{\circ}\text{C}$ ) was 21.6 in April and 23.1 in May at China Camp, and 21.3 in April and 24.4 in May at Mt. Tamalpais.

#### Floral Characters: Size, Pollen Grain Number, and Accessibility

We compared the two species for aspects of their floral biology important to pollinator attraction, reward, and utilization. To compare flower sizes, we took three measurements per flower ( $n = 10$  flowers for *Genista*,  $n = 14$  for *Cytisus*): length of the keel petal, width of the keel petal, and height of the banner petal. The approximate volume of each flower was calculated as a polyhedron with the banner and keel acting as two planes at right angles, with a third connecting plane (Fig. 1).

To quantify pollen production, we collected a single, unopened bud from each of 16 *Cytisus* (6 Mt. Tamalpais, 10 China Camp) and 19 *Genista* (7 Mt. Tamalpais, 12 China Camp) plants. We suspended and sonicated fully dehiscent anthers in a 1% saline solution. We then estimated the number of pollen grains per flower using an Elzone 280-PC electronic particle counter (Micromeritics, Norcross, GA).

Larger flowers might be more difficult to trip open, limiting access to the flower by smaller pollinators. To quantify the force required to open the flowers, we hung paper clips sequentially from the keel petals until the flower was tripped open. The paperclips were then weighed and the total mass converted to force. Unpaired t-tests were used to compare the two species for all floral characters.

#### Visitation Rates to *Cytisus* and *Genista*

Flowers can be tripped only once, after which they remain in an open position. In order to determine the proportion of flowers tripped (an index of visitation), we marked branches on five individuals

of each species at the two sites. From March 19 through May 21, at one- to two-week intervals, we examined every flower on each branch, recording the number of tripped and untripped flowers. We then marked every open flower with Wite-Out<sup>®</sup> to avoid recounting the same flowers at the next census. Wite-Out<sup>®</sup> had no negative effect on fruit production (Parker and Haubensak 2002). Some untripped flowers may have been tripped after being marked and counted (as untripped), leading to an underestimate of the tripping rate. However, we chose this method over the alternative (regular censuses without marking flowers), because floral longevity differs between tripped and untripped flowers, leading to the possibility that untripped flowers would be double-counted more often than tripped flowers, if not marked. We summed the number of tripped flowers and untripped flowers over the entire flowering season (mean flowers per plant = 55 for *Cytisus*, 153 for *Genista*), then calculated the total proportion tripped. We used ANOVA to test for differences among plant species and sites, with both species and site treated as fixed effects. For comparison, we plotted the data alongside results from a similar study done in 1997 (Parker and Haubensak 2002).

#### Pollinator Observations

Throughout the flowering season of 2000 (March 19–May 21), we observed pollinators of *Cytisus* and *Genista* at the two sites. The two sites were visited alternately, either on the same day or on consecutive days, and observations were made during sunny, warm conditions between 9:00 a.m. and 6:00 p.m. In all, we completed 72 hours of observation (36 hours at each site), over 17 days. To maximize our sample size under low visitation rates, we walked haphazard (non-random) transects through the sites, watching and listening for flying insects. We focused on areas where we could see both plant species from the transect. A three-way (pollinator, plant, site) log linear model was used to test for homogeneity of preferences of the two pollinators (Sokal and Rohlf 1995).

For each pollinator, we recorded each attempt to trip a flower, whether that flower was successfully tripped, whether the next flower visited was on the same or a different individual plant, and the distance to the subsequent plant. We calculated the proportion of flowers tripped and the mean number of flowers per plant for each pollinator observed, then averaged these across pollinators for each pollinator type and each plant species. Only two *Bombus* individuals were observed visiting *Cytisus*, therefore we could not do a full, two-way analysis using plant species and insect species as factors. Instead, we compared the two plant species for the behavior of *Apis* only, and compared the two pollinator species for *Genista* only. Because the variables (proportion successfully tripped and number

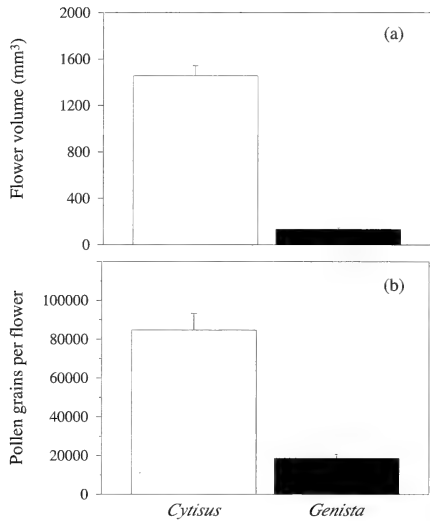


FIG. 2. Floral traits for *Cytisus* and *Genista*: (a) Mean estimated flower volume ( $n = 14$  and  $10$  for *Cytisus* and *Genista*, respectively) and (b) mean number of pollen grains per flower ( $n = 16$  and  $19$ ). Error bars represent 1 SE.

of flowers tripped per plant) were not normally distributed, we analyzed the data using nonparametric Mann-Whitney U tests.

We collected specimens of each pollinator species and identified them following Thorp et al. (1983).

RESULTS

Flower Size, Pollen Grain Number, and Accessibility

*Cytisus* flowers were significantly larger than *Genista* flowers; length of the keel petal ( $\text{mm} \pm 1 \text{ SD}$ ) was  $18.8 \pm 1.4$  compared to  $6.7 \pm 0.5$  for *Genista* ( $df = 22$ ,  $t = 27.1$ ,  $P < 0.0001$ ). The estimated volume of *Cytisus* flowers ( $1450 \text{ mm}^3 \pm 364 \text{ SD}$ ) was an order of magnitude larger than that

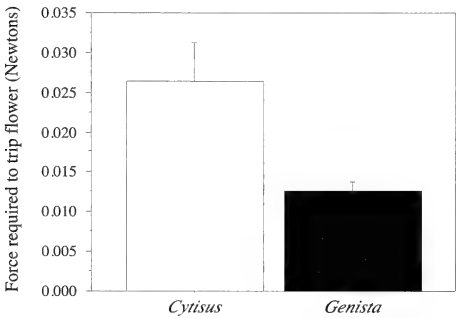


FIG. 3. Force required to access (trip open) flowers of *Cytisus* and *Genista*, determined with a mechanical assay. Error bars represent 1 SE.

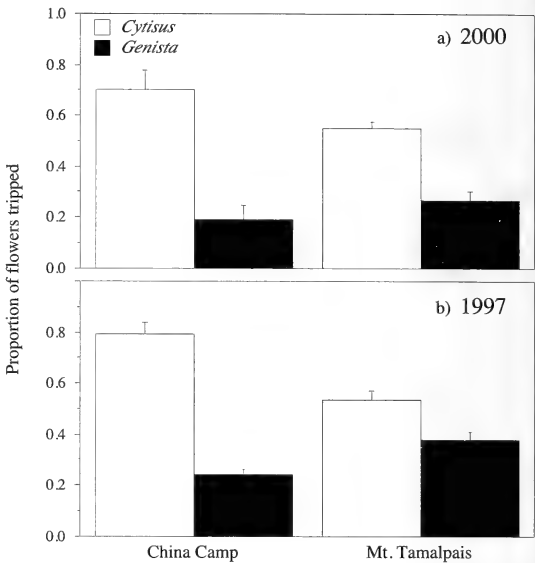


FIG. 4. Proportion of flowers tripped for *Cytisus* (open bars) and *Genista* (filled bars) in two populations. a) Data from 2000, collected from 5 individuals per population; b) Data from 1997, collected from 40–60 individuals per population. Data from 2000 redrawn from Parker and Haubensak (2002). Error bars represent 1 SE.

for *Genista* ( $132 \pm 27$ ; Fig. 2;  $df = 22$ ,  $t = 11.4$ ,  $P < 0.0001$ ). *Cytisus* produced more than four times as many pollen grains per flower as *Genista* (Fig. 2,  $df = 33$ ,  $t = 8.0$ ,  $P < 0.0001$ ).

In the mechanical assay, the two species required significantly different amounts of force to trip the flowers ( $df = 56$ ,  $t = 2.80$ ,  $P = 0.007$ ). We used more than twice as much force in opening flowers of *Cytisus* ( $0.026 \text{ N} \pm 0.005 \text{ SD}$ ) as in opening flowers of *Genista* ( $0.013 \pm 0.006$ ) (Fig. 3).

Visitation Rates to *Cytisus* and *Genista*

At both sites, large-flowered *Cytisus* had a significantly higher proportion of tripped flowers than did small-flowered *Genista* (Fig. 4a, Table 1). These results from the 2000 season confirmed the same pattern seen in 1997 (Fig. 4b, Parker and Haubensak 2002). Therefore, the greater pollination success of *Cytisus* seems to be generalizable over both space and time. There was no significant main effect of site (Table 1). Rather, for *Cytisus*, more

TABLE 1. ANALYSIS OF VARIANCE OF PROPORTION OF FLOWERS TRIPPED (I.E., VISITED) OVER THE ENTIRE SEASON FOR *CYTISUS* AND *GENISTA* AT TWO SITES.

Source	df	SS	F	P
Species	1	0.80	61.1	<0.0001
Site	1	0.01	0.53	0.48
Species $\times$ Site	1	0.07	5.07	0.039
Residual	16	0.21		

TABLE 2. NUMBERS OF POLLINATORS OBSERVED IN 72 HOURS OF OBSERVATION AT TWO SITES ON THE MARIN PENINSULA. Observations were done along haphazard transects through the sites, in areas where both plant species were within visual and auditory range.

Insect species	Mt. Tamalpais		China Camp	
	<i>Cytisus</i>	<i>Genista</i>	<i>Cytisus</i>	<i>Genista</i>
<i>Apis mellifera</i>	19	3	7	12
<i>Bombus vosnesenskii</i>	1	15	1	0
<i>Xylocopa californica</i>	0	1	0	0
Total	20	19	8	12

flowers were tripped at China Camp, while for *Genista*, more flowers were tripped at Mt. Tamalpais (Fig. 4a), resulting in a significant population  $\times$  species interaction effect (Table 1).

Pollinator Observations

In 72 hours of observation at the two sites, three bee species were seen pollinating *Cytisus* and *Genista*: *Apis mellifera*, *Bombus vosnesenskii*, and *Xylocopa californica* (Table 2). We observed a total of 59 pollinators, which made 342 effective visits to flowers (in which the flower was tripped). Given that hundreds to thousands of flowers were being watched at any one moment, this represents a very low pollination rate in terms of visits/flower/hour.

*Apis* was the numerically dominant pollinator observed at both sites, although *Genista* at Mt. Tamalpais was visited most by *Bombus* (Table 2). *Xylocopa* was observed only once and is left out of subsequent analyses. Results of the three-way log linear model indicated that bee species preferences for the two broom species differed across the two sites ( $G[\text{Williams}] = 8.18$ ,  $df = 3$ ,  $P < 0.005$ ). Therefore, we examined these preferences for each site separately. At Mt. Tamalpais, *Apis* primarily visited *Cytisus*, while *Bombus* primarily visited *Genista* ( $G[\text{Williams}] = 26.48$ ,  $df = 1$ ,  $P < 0.001$ ). At China Camp, there were too few *Bombus* visits to include in the analysis, but a chi-square test indicated that *Apis* had no significant preference for *Cytisus* or *Genista* (chi-square = 1.32,  $df = 1$ ,  $P > 0.10$ ). Therefore, we did not find evidence to support the prediction that the small-flowered *Genista* was accessible to a greater number of pollinator species. Nor did we find that the larger pollinators (*Bombus*) tended to visit the larger flowers (*Cytisus*).

Before flying to a new individual, bees (all species combined) visited on average 6.6 ( $\pm 10.6$ ) flowers/plant of *Cytisus* and 3.9 ( $\pm 3.8$ ) flowers/plant of *Genista*, a difference that was not statistically significant ( $Z = 0.25$ ,  $P = 0.80$ ). When considered alone, *Apis* did not differ in its pattern of movement on the two plant species (Fig. 5,  $Z = 0.22$ ,  $P = 0.83$ ). Although *Apis* tended to visit more flowers per plant than *Bombus* (Fig. 5), this differ-

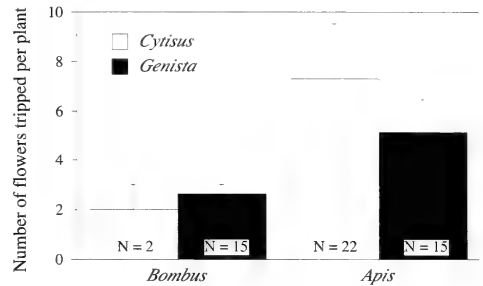


FIG. 5. Number of flowers successfully visited (tripped) per individual plant before flying to a new plant, for *Bombus* observed on *Cytisus* ( $n = 2$ ) and *Genista* ( $n = 15$ ) and *Apis* observed on *Cytisus* ( $n = 22$ ) and *Genista* ( $n = 15$ ). Error bars represent 1 SE.

ence was not statistically significant (*Genista* only,  $Z = 1.20$ ,  $P = 0.23$ ).

We used *Apis* visitation success (ratio of flowers tripped to flowers attempted) as a measure of the accessibility of the two flower types; pollinators were more successful at accessing flowers of the small-flowered *Genista* than the large-flowered *Cytisus* (Fig. 6, *Apis* only,  $Z = 2.13$ ,  $P = 0.03$ ). The proportion of *Genista* flowers successfully tripped did not differ for the two pollinator species (Fig. 6,  $Z = 1.0$ ,  $P = 0.32$ ). The proportion of *Cytisus* flowers successfully tripped appeared to be higher for *Bombus* than for *Apis* (Fig. 6). This difference was statistically significant ( $Z = 2.09$ ,  $P = 0.03$ ), but the small sample size for *Bombus* ( $N = 2$ ) suggests caution in interpreting this result.

DISCUSSION

Do Floral Characters Predict Which Invasive Plants Should Be Most Attractive to Pollinators and Which Should Be Most Pollen Limited?

We started with two alternative hypotheses for how floral traits could affect pollinator attraction and visitation in this system. The first hypothesis

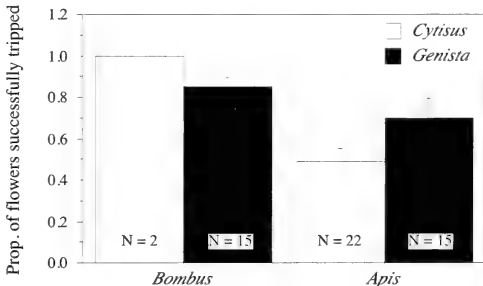


FIG. 6. The mean proportion of flower visits attempted in which the flower was successfully tripped open, for individual *Bombus* and *Apis* pollinators observed at flowers of *Cytisus* (open bars) or *Genista* (filled bars). Each pollinator observed could involve visits to flowers on one plant or multiple plants. Error bars represent 1 SE.



predicted that because of the unusual "tripping" mechanism in these two species, the larger *Cytisus* flowers could be more difficult for pollinators to handle, which would reduce the number of insect species capable of visitation. *Cytisus* would then be relatively specialized on larger insects, and pollinator limitation should be more prevalent in *Cytisus* than in *Genista* (assuming an equal and variable pool of pollinator species for the two plants). In fact, we did find evidence that *Cytisus* flowers are more difficult to access than *Genista* flowers, both from our mechanical assay and from observations of *Apis* visitation. However, this difference did not result in a difference in the pollinator assemblage for the two plants. We did not find that small solitary bees or flies visited *Genista*, although they are common in the area (G. Lebuhn, personal communication), and we did not find that larger bees specialized on *Cytisus*. Rather, while *Apis* commonly visited both plant species, the larger *Bombus* and *Xylocopa* visited primarily *Genista*. Recent work in Great Britain (Stout 2000) found that very large *Bombus* individuals (>20 mm) were less adept at accessing *Cytisus* flowers than were smaller *Bombus*. This suggests, in concert with our results, that the largest bees may have trouble handling *Cytisus* flowers and may in fact prefer *Genista* flowers.

While we did not find that the differences in floral accessibility between the two invaders translated to an effect on pollinator composition in Marin County, this effect could be important in other systems. For example, one of us (Parker 1997) observed that *Cytisus* was rarely successfully tripped by *Apis* in Washington State. Temperature can affect floral accessibility: *Cytisus* flowers are more difficult to trip in cold compared to warm temperatures in the lab (B. Burley, R. Martin, and K. M. Karoly unpublished data). The Washington research suggests that in colder climates, the difficulty of tripping *Cytisus* flowers could contribute to pollen limitation.

Our second hypothesis postulated that pollinator visitation would be based on floral attractiveness. The prediction was that the larger flowers and greater pollen rewards of *Cytisus* could increase its attractiveness to pollinators, increasing its success in competing with resident plants for pollinator services relative to *Genista*. We found, both in 1997 and 2000, that visitation rates to the two plant species were consistent with this hypothesis. *Cytisus* flowers were more frequently tripped in both years and at both study sites. Given that *Genista* tends to produce more flowers than *Cytisus* on plants of the same size (Parker and Haubensak unpublished data), pollinators in this study appeared to be more attracted by the rewards of single flowers than by the size of the overall display.

*Genista* might have ways of compensating for its lower pollinator visitation. Small flowers sometimes represent reduced allocation to attraction in an evolved syndrome including increased selfing

and autogamy and lower inbreeding depression (Piper et al. 1986; Rathcke and Real 1993; Parker et al. 1995; Brunet and Eckert 1998). *Genista* does not exhibit high levels of autogamy (Parker and Haubensak 2002). However, compared to *Cytisus*, it does show less inbreeding depression at seed-set, consistent with the syndrome of increased selfing and decreased allocation to attractive structures (Parker and Haubensak 2002). Thus when pollinators tend to visit multiple flowers on a plant, *Genista* may be able to take advantage of those visits more effectively than *Cytisus*.

#### *Are Plants Better "Matched" to Pollinators from Their Native Range?*

If the floral traits of plants have evolved in response to pollinators in their native range, one might expect to see that a pollinator introduced from the same region as an introduced plant would be a higher quality pollinator, or better match, for that plant. We found no evidence to support this prediction in our study. *Apis mellifera*, native to Europe, was not better at tripping flowers than the locally native *Bombus vosnesenskii*. We did not follow the fate of each tripped flower to determine relative pollen transfer and fruit set for the different pollinators (see Schemske and Horvitz 1984). However, the European *Apis* and native *Bombus* did not differ significantly in their tendency to promote outcrossing by moving between plants instead of within plants.

Given that most plant-pollinator interactions are thought to have arisen from diffuse coevolution of guilds rather than coevolution between pairs of species (Jordano 1987; Pellmyr 1992), these findings are not particularly surprising. European species of *Bombus* probably occurred throughout the evolutionary history of these broom species, and may have influenced the evolution of their floral morphology, and North American and European *Bombus* are probably similar in terms of their pollination value to broom. Although we lack extensive information about the degree to which *Cytisus* and *Genista* are pollinated by *Apis* in their native range, one recent study in Great Britain recorded that flowers of *Cytisus* there were tripped primarily by *Bombus*, while *Apis* only visited previously tripped flowers (Stout 2000). More comparative studies of plant-pollinator interactions in native vs. introduced ranges are needed to better understand the role of these mutualisms in the invasion process. We are aware of only one case in which a highly specific pollinator was left behind during invasion (e.g., fig wasp invasion in Florida, Nadel et al. 1992).

#### *Invasional Meltdown?*

Both *Cytisus* and *Genista* can be pollen limited (Parker 1997; Parker and Haubensak 2002); therefore, attracting pollinators plays a critical role in assuring reproduction. We found that both native



and non-native insects pollinate these invaders. *Apis mellifera*, native to Europe, was by far the dominant visitor at the China Camp site, and was also more common than *Bombus* at Mt. Tamalpais. It has recently been suggested that positive interactions among invaders may commonly facilitate new invasions or exacerbate the spread or impacts of established invaders, leading to non-linear “invasional meltdown” (Simberloff and Von Holle 1999). In our system, an introduced pollinator appears to be facilitating the invasion of two introduced shrubs.

Recent concern over the environmental impacts of *Apis* introduction has focused on the fates of native pollinators (Roubik 1982; Buchmann and Nabhan 1996; Goodell 2000). We point to another potential conservation issue, the effect of *Apis* introduction on the spread of noxious weeds in natural ecosystems. In keeping with this warning, recent work by Barthell et al. (2001) found that pollination by *Apis* contributed up to half of the seed produced by the noxious invader *Centaurea solstitialis* (yellow star thistle) in California. Beekeeping is common at the suburban-rural interface. The bees at our sites may have come from feral colonies, or beekeepers may have been responsible for domestic colonies in nearby residential or agricultural areas. In light of the results presented here, the potential negative impacts of beekeeping on weed management should play a role in policy decisions having to do with local introduction and control of *Apis* colonies.

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## FOXTAIL PINE IMPORTANCE AND CONIFER DIVERSITY IN THE KLAMATH MOUNTAINS AND SOUTHERN SIERRA NEVADA, CALIFORNIA

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### ABSTRACT

We sampled 15 foxtail pine stands located in the central ridges of the Klamath Mountains in order to estimate conifer density, basal area, and importance values. We compared these estimates to previous research in the southern Sierra Nevada. Our analyses revealed a lack of interregional divergence of stand characteristics between the Klamath Mountains and southern Sierra Nevada despite subspecific designation and recently identified genetic divergence. Bray-Curtis ordination and hierarchical cluster analyses identified four stand types—1) stands dominated by foxtail pine, 2) stands with foxtail pine and whitebark pine, 3) stands with foxtail pine and red fir, and 4) mixed stands with foxtail pine, red fir, and western white pine. Sub-regions within the Klamath Mountains differed in foxtail pine relative density, conifer diversity, and substrate heterogeneity. Further analyses of the Klamath Mountains stands identified an inverse relationship between foxtail pine importance and conifer diversity. Interactions between the mountain island effect and substrate heterogeneity were inferred as regulatory mechanisms for foxtail pine importance and conifer diversity, but further research is needed to determine causal relationships from our correlations.

Key words: foxtail pine, conifer diversity, mountain island effect, substrate heterogeneity, Klamath Mountains

Foxtail pine (*Pinus balfouriana* Grev. & Balf.) is a California endemic conifer found in two isolated areas of the state separated by 500 kilometers. In extreme northern California it grows in the central ranges of the Klamath Mountains, while the southern population is centered on the Cottonwood Basin and surrounding areas in the southern Sierra Nevada. The Scottish botanist and explorer John Jeffery discovered it in 1852 on a botanical reconnaissance of the Klamath Mountains. Professor John H. Balfour and Dr. R. K. Greville subsequently prepared the original description and illustrations for the Oregon Association (Mastrogriuseppe 1972). Since its discovery, however, there has been a paucity of ecological research into the biology of this subalpine tree. Ball (1976) highlights the need for research into the factors determining the ecological patterns of foxtail pine.

Foxtail pine is a five-needle haploxyton pine placed within the subsection *Balfourianae* Engelm. along with Great Basin bristlecone pine (*Pinus longavea* D. Bailey) in the western Great Basin and the Rocky Mountain bristlecone pine (*Pinus aristata* Engelm.) in the eastern Great Basin and Rocky Mountains. Mastrogriuseppe (1972) argued that two allopatric subspecies of foxtail pine exist upon differences in mean cone length, seed wing length, cotyledon number, and needle resin duct spacing. Mastrogriuseppe and Mastrogriuseppe (1980) subse-

quently named the southern population *Pinus balfouriana* ssp. *austrina*.

An 11 loci allozyme analysis of stands within the northern population revealed high levels of genetic differentiation among stands (Oline et al. 2000). This genetic diversity was significantly greater than the differentiation between the northern and southern populations and was hypothesized to be a function of the mountain island effect, genetic drift, possible serpentine soil adaptation, and high conifer richness (Hamrick et al. 1994; Oline et al. 2000).

Foxtail pine and Great Basin bristlecone pine from the White Mountains exhibit strong anatomical and morphological similarities suggesting hybridization (Mirov 1967; Bailey 1970). Successful experimental crosses support this proposed hybridization based on morphological continuity (Critchfield 1977). Numerous hypotheses concerning the origin of the subsection *Balfourianae*, foxtail pine, and its subspecies have been offered (Mastrogriuseppe 1972; Critchfield 1977; Raven and Axelrod 1978). Most hypotheses, however, date the initial divergence of the bristlecone/foxtail pine ancestor to the Oligocene and the disjunction of foxtail pine within California to the Xerothermic period of the Holocene approximately 8000 years ago (Critchfield 1977; Raven and Axelrod 1978) or the Sierran orogeny approximately 2 million years ago (Mirov 1967; Bailey 1970).

Population and community-level research on foxtail pine is sparse. This pine is intolerant of shade at all stages of growth, an inhabitant of various high elevation substrates, and is a major to minor component of subalpine forests and wood-

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lands in both the Klamath Mountains and southern Sierra Nevada (Ryerson 1983; Sawyer and Thornburgh 1988). Extreme old age is achieved on xeric high altitude locations and trees can reach a maximum age of approximately 2000 years in the southern population (Ball 1976; Scuderi 1987). Trees from the northern population, however, only attain maximum ages of approximately 800 to 1,000 years as a result of widespread heart rot and periodic fire (Mastrogiosuppe 1972).

Foxtail pine typically occurs in low diversity stands with whitebark pine (*Pinus albicaulis* Engelm.), lodgepole pine (*Pinus contorta* Loudon ssp. *murrayana* Critchf.), western white pine (*Pinus monticola* Douglas), red fir (*Abies magnifica* Andr. Murray), and mountain hemlock (*Tsuga mertensiana* Carriere) (Mastrogiosuppe 1972; Ryerson 1983). Common ground layer associates include dry site graminoids, herbs, and shrubs such as *Agrostis*, *Arabis*, *Arcotostaphylos*, *Carex*, *Ceanothus*, *Eriogonum*, *Festuca*, *Juncus*, and *Sedum* (Ryerson 1983; Sawyer and Keeler-Wolf 1995).

Foxtail pine in the Klamath Mountains forms extensive stands at high elevations on isolated peaks and ridges with mafic and ultramafic substrates where it is the dominant tree. Exceptions occur in the China Peak and Russian Peak areas where it is associated with as many as six other conifer species in a mixed subalpine forest type (Sawyer and Keeler-Wolf 1995). Conifers such as Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), incense-cedar (*Calocedrus decurrens* (Torrey) Florin), and Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) form a minor component in these stands. In the southern Sierra Nevada, foxtail pine forms extensive low diversity stands at high elevations on granitic and metamorphic substrates. Common associates include whitebark pine, limber pine (*Pinus flexilis* James), red fir, and western white pine as described by Vankat (1970) in Sequoia National Park as a foxtail pine forest type.

Limited research suggests that foxtail pine's distribution is determined by variation in substrate, climate, and interspecific interactions with other conifers (Mastrogiosuppe 1972; Ryerson 1983; Scuderi 1987; Oline et al. 2000). The low competitive ability of foxtail pine and the high regional conifer species richness of the Klamath Mountains may illustrate restriction of foxtail pine to safe sites on ultramafic substrates and granitic boulder fields where shade tolerant conifers cannot shade out intolerant foxtail pine trees (Ryerson 1983; Sawyer and Thornburgh 1988).

Previous research has identified examples of ecological differences between the two populations. Foxtail pine stands in the southern Sierra Nevada achieve their highest densities on northern slopes (Ryerson 1983), which contradicts the typical southern and eastern slope success observed in the Klamath Mountains (Mastrogiosuppe 1972). Surprisingly the range of foxtail pine, commonly de-

scribed as a Pleistocene relict, has been documented as expanding to lower elevations in the southern Sierra Nevada (Ryerson 1983). This expansion may be a function of climate change, low conifer richness, demographic and environmental stochasticity, or a combination of these processes (Mastrogiosuppe 1972; Ryerson 1983; Scuderi 1987).

We documented environmental and compositional gradients related to the level of dominance of foxtail pine among stands in the Klamath Mountains. We also compared these stands to those of the southern Sierra Nevada using the studies of Vankat (1970) and Ryerson (1983). These comparisons allowed us to analyze the disjunct foxtail pine populations at several levels and to make inferences about the role of interspecific interactions, geologic substrate, and climate in the distribution and dominance of foxtail pine at the intraregional and local levels in the Klamath Mountains.

## METHODS

**Study areas.** The Klamath Mountains are composed of a complex set of predominantly southwest to northeast trending mountain ridges separated by deep canyons and valleys that encompass approximately 30,300 km<sup>2</sup> of northern California (Fig. 1). The main mountain ranges, from south to north, are the South Yolla Bolly Mountains, North Yolla Bolly Mountains, Trinity Alps, Salmon Mountains, Scott Mountains, Trinity Mountains, Marble Mountains, and Siskiyou Mountains. Summits average from 1500 to 2100 m in elevation, with a maximum of 2750 m at Mount Eddy. The major watersheds include the Sacramento, Trinity, Salmon, Scott, Klamath, and Smith Rivers. Climate patterns conform to a modified mediterranean climate type with long, wet winters and generally dry summers. Average precipitation ranges from 125 cm to 175 cm, with thunderstorms and lightning developing in late August and early September (Major 1988). Plant assemblages range from low elevation chaparral, woodlands and forests, to patches of alpine plants, with a number of endemic and relict populations of vascular plants on ultramafic substrates (Walker 1954; Kruckeberg 1992).

The southern Sierra Nevada is a linear northwest-southeast trending mountain range bounded on the west by the San Joaquin Valley and on the east by the White Mountains and the Great Basin (Fig. 1). Over 285 peaks reach elevations of 3600 m, over 140 exceed 3900 m, while 11 peaks top 4200 m (Kruse 1990). Major watersheds include the many forks of the Kern, Kings and San Joaquin Rivers. Regional climates are influenced by local topography, but all resemble a modified Mediterranean climate with moderately wet winters and dry summers broken by periods of afternoon thunderstorms. Annual precipitation ranges from 35 cm to 115 cm on the western crest and from 50 cm to 75 cm on the eastern crest (Major

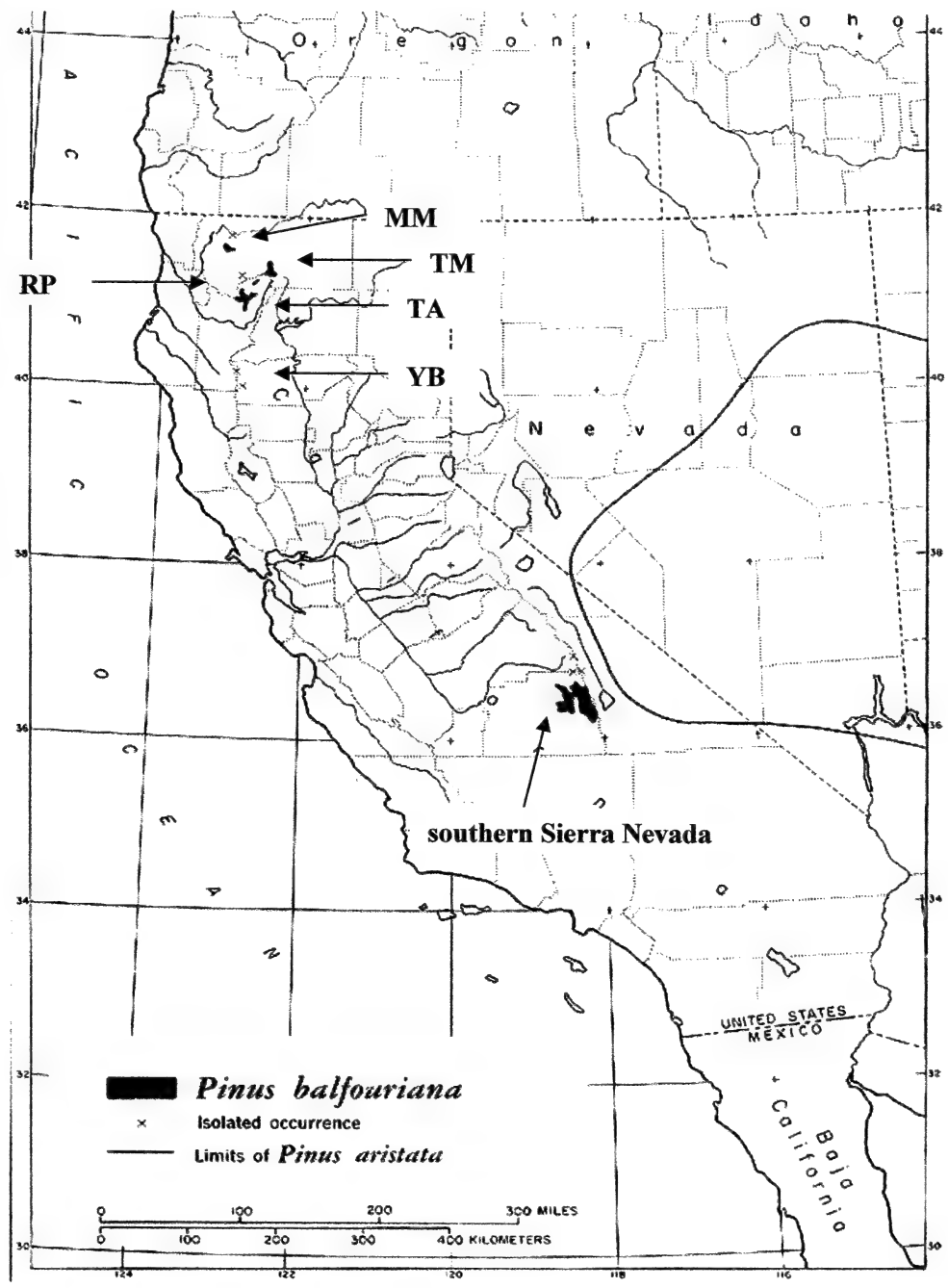


FIG. 1. Distribution of foxtail pine in the Klamath Mountains and Sierra Nevada by Griffin and Critchfield (1972). MM = Marble Mountains, RP = Russian Peak, TA = Trinity Alps, TM = Trinity Mountains, YB = Yolla Bolly Mountains.

1988). Plant assemblages range from low elevation pinyon pine woodlands to alpine tundra on the eastside and from foothill woodlands, montane and subalpine forests, to alpine vegetation types on the westside.

*Sampling techniques.* We identified five sub-regions where foxtail pine was dominant within the Klamath Mountains—the Yolla Bolly Mountains, the Trinity Alps, the Trinity Mountains, Russian Peak, and the Marble Mountains (Table 1). Each

TABLE 1. SUB-REGIONAL LOCALITIES OF 15 FOXTAIL PINE STANDS IN THE KLAMATH MOUNTAINS. SUB-REGIONS AND LOCALITIES WERE BROADLY DEFINED AND DO NOT HAVE DISTINCT BOUNDARIES.

Sub-region	Locality	Stands
Marble Mountains	Lake Mountain	2
Russian Peak	Russian Peak	1
Trinity Alps	Granite Peak	2
	Seven-Up Peak	1
	Union Creek	2
Trinity Mountains	Mt. Eddy	2
	China Mountain/ Crater Lake	2
Yolla Bolly Mountains	North	2
	South—Mt. Lynn	1

sub-region contained distinct localities where fox-tail pine density was sufficiently high for sampling. At each locality we randomly identified stands primarily through homogeneity of species composition and secondarily through homogeneity of geomorphology. Stand areas ranged from 8 ha to 28 ha. A total of 15 stands were sampled from the 10 localities in the 5 sub-regions from May 22 through September 16, 2000.

We used the point centered quarter (PCQ) method to sample each of the 15 stands in order to estimate tree density, basal area, frequency, and importance values by species. This method is a plot-less sampling technique based upon the placement of random points along pre-determined transects perpendicular to contour lines within each stand. Trees were defined as single conifer individuals with diameter measured at breast height for trees taller than 1.37 m, at ground level for trees below 1.37 m in height, and as an average for trees with multiple trunks.

Ryerson (1983) sampled 15 marginal foxtail pine stands located in the southern Sierra Nevada using the PCQ method in a similar manner to estimate conifer importance values. Vankat (1970) conducted linear transect sampling of foxtail pine forest type within Sequoia National Park to estimate stand and species-specific tree density, basal area, and frequency.

To determine the number of points needed to adequately estimate stand density, we conducted pre-sampling of two stands in the North Yolla Bolly Mountains following Bonham's (1989) method. We determined that 22 points were adequate to estimate stand-level parameters with an error of 10%. We increased this number to 25 to ensure reliable estimation, but were only able to establish 15 points in the Marble Mountains stands due to their small size.

To generate estimates of tree density, basal area, and frequency, we placed 25 points along four to six transects that were evenly spaced throughout the stand. Spacing among points was dependent upon stand area. We followed Bonham's (1989)

protocol at each point, yielding 100 sampled trees per stand. The diameter at breast height (DBH) was measured for each tree, and the average diameter and stem number were obtained for trees with multiple trunks. We measured percent slope, aspect, elevation, and identified bedrock type. Cover of boulders (>50 cm), cobbles (10 cm–50 cm), gravels (<10 cm), and organic material was estimated using the Braun-Blanquet scale (Bonham 1989).

*Estimators and statistical analyses.* The PCQ method allowed unbiased estimation of tree density and basal area within each stand (Pollard 1971). From these values we calculated stand and species-specific tree density, basal area, frequency, and importance values (Kent and Coker 1992). Importance values are composite estimates based upon the summation of relative estimates of species density, frequency, and basal area (Bonham 1989). These values could therefore range from a minimum of zero, if the tree species was absent, to a maximum of 300 if it was the only species present.

We placed foxtail pine trees into ten size classes based upon diameter measurements. Using a simple linear regression model constructed from tree ring counts obtained from Mastrogiuseppe (1972), we related logarithmically transformed values of tree diameter to age by the following equation:

$$\text{Log}(\text{age}) = 1.1571(\text{Log}[\text{DBH}]) + 0.3762 \quad (1)$$

This model was significant (ANOVA:  $F_{1,43} = 277.0459$ ,  $P = 0.000001$ ) and had a high degree of explanatory power ( $R^2 = 0.8738$ ). Hundred-year age classes could be correlated to size classes with confidence and reproductive success inferred from relative density of the first age class (Ryerson 1983). Survival among age classes was calculated as the ratio of the density of age class  $x$  to the density of age class  $x + 1$ .

We used the Shannon-Wiener Index ( $\log_{10}$ ) to measure substrate heterogeneity and tree diversity using median species-specific relative density values for conifer diversity. We computed Jaccard similarity coefficients, weighted by species-specific importance values, among all stands to obtain average within and among sub-regional stand similarities within the Klamath Mountains. We subjected the data to a variety of statistical analyses. Significance levels for hypothesis tests were set at  $\alpha = 0.05$  or 0.10. A modified t-test checked for significant differences among index values (Zar 1999). Two-sampled t-tests and Mann-Whitney U tests established interregional differences and similarities for stand characteristics using Ryerson's (1983) and Vankat's (1970) data sets. Variation around the mean of these estimates, if the data were normally distributed, was compared between regional populations using Hartley's equal variance test. We used simple linear regression analyses and General Linear Models (GLM) ANOVA's to identify trends within and differences among stand characteristics and environmental variables by sub-regions within the Klamath

TABLE 2. SUMMARY OF THE ENVIRONMENTAL VARIABLES AND STAND CHARACTERISTICS OF 15 FOXTAIL PINE STANDS FROM THE KLAMATH MOUNTAINS BY SUB-REGIONS. Conifer diversity and substrate heterogeneity are reported as Shannon-Wiener Index ( $\log_{10}$  base) values. Density given in trees/hectare and basal area in  $\text{m}^2/\text{hectare}$ .

Stand	Density	Basal area	Area (ha)	Elevation (m)	Aspect	Slope (%)	Substrate heterogeneity	Conifer diversity	Conifer richness
Yolla Bolly Mountains									
1	238	45	8.6	2365	WSW	28.0	0.09	0.39	3
2	51	10	25.4	2260	WSW	39.7	0.38	0.44	5
3	85	14	15.3	2335	NNW	42.6	0.18	0.31	3
Trinity Alps									
4	192	25	10.1	2240	WSW	29.0	0.29	0.42	5
5	257	27	11.4	2345	WNW	39.6	0.29	0.44	5
6	133	36	28.0	2295	WNW	59.3	0.29	0.26	3
7	112	27	11.2	2202	WNW	40.1	0.25	0.42	3
8	190	38	28.0	2004	NNE	15.3	0.41	0.52	6
Trinity Mountains									
9	252	44	47.5	2358	WNW	25.8	0.33	0.52	6
10	207	8	24.5	2376	SSE	32.9	0.41	0.61	6
11	92	26	28.1	2500	WNW	55.7	0.41	0.42	5
12	381	21	14.0	2205	ESE	7.2	0.41	0.69	6
Russian Peak									
13	315	24	12.8	2180	NNW	33.1	0.44	0.84	8
Marble Mountains									
14	171	25	8.2	2003	SSE	31.5	0.41	0.66	6
15	198	10	3.1	2033	NNE	35.0	0.20	0.50	6

Mountains. Average within and among sub-regional Jaccard similarity coefficients were compared using GLM ANOVA with Fischer's LSD grouping algorithm among sub-regions with more than two stands.

We used hierarchical cluster and Bray-Curtis ordination analyses to reduce dimensionality within the data sets and to analyze multivariate correlations among stand compositional and environmental variables (Kent and Coker 1992). Hierarchical cluster analyses provided dendrograms based on Euclidean distance, scaled by standard deviations, using species importance values. Clusters were identified with the group average (unweighted pair-groups) algorithm. We employed Bray-Curtis ordination analyses to evaluate the results of the hierarchical cluster analyses and to correlate stand groupings with environmental variables using the Sorenson similarity coefficient based upon species importance values. Biplots were overlain with compositional and environmental variable vectors and correlations with the first two axes were computed (McCune 1993).

## RESULTS

**Summary.** Approximately 1,420 trees were sampled in the determination of importance values for 11 conifer species sampled within 15 stands located in the Klamath Mountains. Stand densities ranged from 50 trees/ha in the North Yolla Bolly Mountains to 381 trees/ha at China Mountain (Table 2). Stand basal area ranged from a minimum of 8  $\text{m}^2/\text{ha}$  at China Mountain to a maximum of 45  $\text{m}^2/\text{ha}$  at Mt. Lynn (Table 2). Foxtail pine was the most

important conifer in 14 out of the 15 stands with a regional average importance value of 168, a minimum of 46 at Crater Lake, and a maximum of 241 at Seven-Up Peak (Table 3). The first age class (<100 years) dominated ( $\geq 50\%$  relative density) the age class distribution of foxtail pine in 9 out of 15 stands. Maximum tree age approached 1000 years for a few foxtail pine trees scattered throughout stands. Average stand abundances by age class within the Klamath Mountains assumed J-shaped distributions and differed (ANOVA:  $F_{9,1411} = 120.06$ ,  $P = 0.000001$ ). This pattern was also observed in the southern Sierra Nevada (Ryerson 1983).

**Klamath Mountains.** The common tree species were foxtail pine, red fir, and western white pine with importance value dependent upon geographic sub-region. Foxtail pine achieved higher densities on steep, high elevation slopes with western aspects (Tables 2, 3). Whitebark pine was primarily found in stands on high elevation peaks with granitic or glacial till substrates. Mountain hemlock tended to be most important on northern slopes at lower elevations and east slopes at higher elevations. Conifers typical of lower elevations, such as incense-cedar, Jeffrey pine, and Douglas-fir, were found in stands with elevations below 2200 m in elevation or western and southern aspects.

Conifer diversity was variable throughout the region, but was greatest in northern-most stands (Table 2). Stands in the Yolla Bolly Mountains and southern Trinity Alps had lower diversity values, while stands in the Trinity and Marble Mountains had higher diversity values. Diversity values ranged

TABLE 3. CHARACTERISTICS OF FOXTAIL PINE WITHIN 15 STANDS FROM THE KLAMATH MOUNTAINS BY SUB-REGIONS. Density given in trees/hectare, basal area in m<sup>2</sup>/hectare, and relative values in percent.

Stand	Density	Relative density	Basal area	Relative frequency	Relative dominance	Importance value
Yolla Bolly Mountains						
1	155	65	38	46	95	207
2	32	63	7	48	89	199
3	62	73	10	56	90	220
Trinity Alps						
4	98	51	13	48	57	156
5	121	47	13	44	51	142
6	109	82	31	61	98	241
7	53	47	20	46	80	173
8	116	61	33	44	81	187
Trinity Mountains						
9	153	61	38	45	96	202
10	79	38	5	33	68	139
11	113	59	21	46	88	193
12	69	18	3	18	10	46
Russian Peak						
13	69	22	9	26	38	85
Marble Mountains						
14	74	43	17	31	89	163
15	109	55	4	40	64	159

from 0.25 at Seven-Up Peak to 0.83 at Russian Peak. These two values were statistically different ( $t_6 = 43.9796$ ,  $P < 0.00001$ ) according the t-test proposed by Hutcheson (1970). Conifer richness was as low as 3 species in the Trinity Alps stands and as high as 8 species in the Russian Peak stand.

Foxtail pine inhabited slopes with a variety of aspects. A large proportion of stands had northwest and southwest aspects with foxtail pine importance higher on southwest facing slopes (Tables 2, 3). Substrate heterogeneity measured with the Shannon-Wiener Diversity Index ranged from a low of 0.09 in the North Yolla Bolly Mountains to 0.44 at Russian Peak (Table 2). Inceptisols developed from mafic and ultramafic geologic substrates were the primary soil type within stands. Pockets of granitic and metasedimentary rocks were prominent in the Yolla Bolly Mountains stands and at Russian Peak. Evidence of glaciation was present in high elevation stands with glacial till as an important substrate at stands in the Trinity Alps, Russian Peak, and Trinity Mountains. Elevations ranged from a low of 2000 m at Lake Mountain to a high of 2500 m at China Peak with a regional average of 2247 m (Table 2).

Simple linear regression analyses identified numerous compositional and environmental gradients among stands located in the Klamath Mountains (Fig. 2). A south to north latitudinal gradient was identified as significantly influencing foxtail pine relative density, conifer diversity, species richness, substrate heterogeneity, and foxtail pine survival to the second age class ( $F_{1,14} > 4.35$ ,  $P < 0.05$ ,  $R^2 > 0.30$ ). Conifer diversity negatively influenced foxtail pine importance (Fig. 2A). Substrate heterogeneity, in turn, was identified as positively influence

ing conifer diversity (Fig. 2B). This relationship was dependent upon Pleistocene glaciation with stands on glaciated surfaces exhibiting a stronger correlation with high conifer diversity (glaciated  $R^2 = 0.6181$ , unglaciated  $R^2 = 0.3002$ ).

GLM ANOVA's of compositional and environmental variables revealed sub-regional differentiation. Elevation, conifer species richness and diversity, whitebark pine relative density, and foxtail pine survival to the second age class significantly differed among the five sub-regions (ANOVA:  $F_{4,11} > 3.25$ ,  $P < 0.05$ ). In general, foxtail pine survival was highest in stands with lower conifer diversity.

Stands were more homogeneous, as measured with average sub-regional Jaccard similarity coefficients, within sub-regions versus among sub-regions (Fig. 3). In general, within sub-region Jaccard similarity coefficients were greater than among sub-region coefficients with the Marble Mountains being similar to all other sub-regions (ANOVA:  $F_{5,127} = 17.50$ ,  $P = 0.0000009$ ). Russian Peak was most similar to the Trinity Mountains and Marble Mountains, while least similar to the Trinity Alps and Yolla Bolly Mountains. Similarity was not correlated to distances among sub-regions, however the extreme northern and southern stands were among the least similar. The recently disturbed stand (e.g., Crater Lake, stand 12) was the least similar to others at both within and among sub-regional levels.

The Bray-Curtis ordination of the Klamath stands differentiated stands with high conifer richness from those with high foxtail pine importance values (Fig. 4). Axis I in the ordination was highly and variously correlated with mountain hemlock ( $R = -0.837$ ), western white pine ( $R = 0.564$ ) and foxtail pine ( $R = 0.547$ ) importance values. Axis II



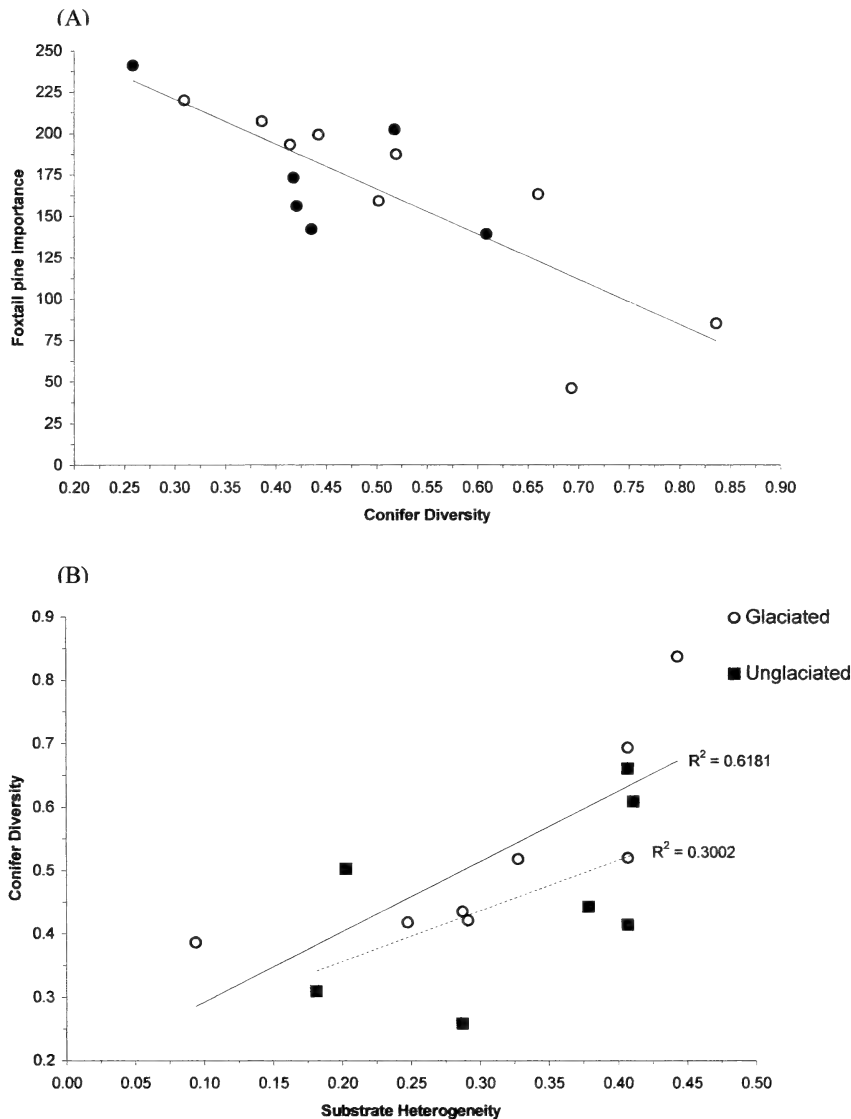


FIG 2. (A) Relationship between conifer diversity and foxtail pine importance ( $F_{1,14} = 23.096$ ,  $P = 0.000343$ ,  $R^2 = 0.6399$ ). Stands with serpentine soils are represented by filled points. (B) Relationship between substrate heterogeneity and conifer diversity grouped by glaciation history (dashed line = unglaci-ated regression, solid line = glaci-ated regression). See text for definitions of conifer diversity and substrate heterogeneity.

was similarly correlated with western pine ( $R = -0.617$ ), whitebark pine ( $R = -0.616$ ), and foxtail pine ( $R = 0.603$ ) importance values. These two axes had relatively high explanatory power ( $R^2 = 0.739$ ). Stands tended to be broadly grouped by sub-region and composition (Fig. 4). Crater Lake was unique with extremely low foxtail pine importance and high conifer species richness. This stand was selectively logged and burned in the last half century.

*Southern Sierra Nevada.* Using Ryerson's (1983) data set, stand density ranged from a low of 72

trees/ha to a high of 881 trees/ha, while stand basal area ranged from a low of 9 m<sup>2</sup>/ha to 646 m<sup>2</sup>/ha (Table 4). Extremely high density and basal area values were associated with whitebark pine dominance and may have been an artifact of sampling trees with numerous trunks. A wide range of importance values for foxtail pine, low species richness, and high elevations characterized these stands (Table 4).

Using Vankat's (1970) data set, stand density ranged from a low of 200 trees/ha to a high of 700 trees/ha, while stand basal area ranged from 15 m<sup>2</sup>/ha

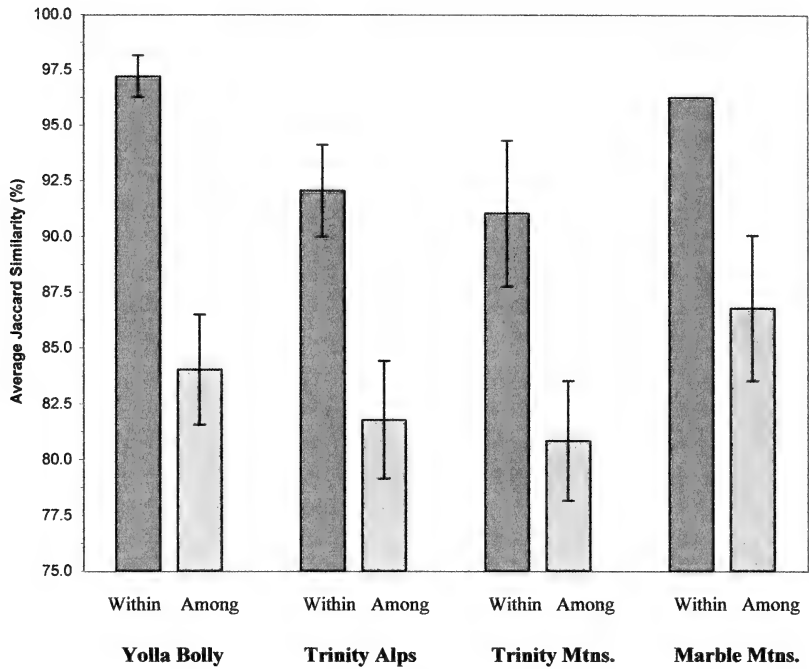


FIG. 3. Comparison of average within and among sub-regional Jaccard similarity coefficients for 15 foxtail pine stands in the Klamath Mountains. Differences are significant (ANOVA:  $F_{5,127} = 17.50$ ,  $P = 0.0000009$ ).

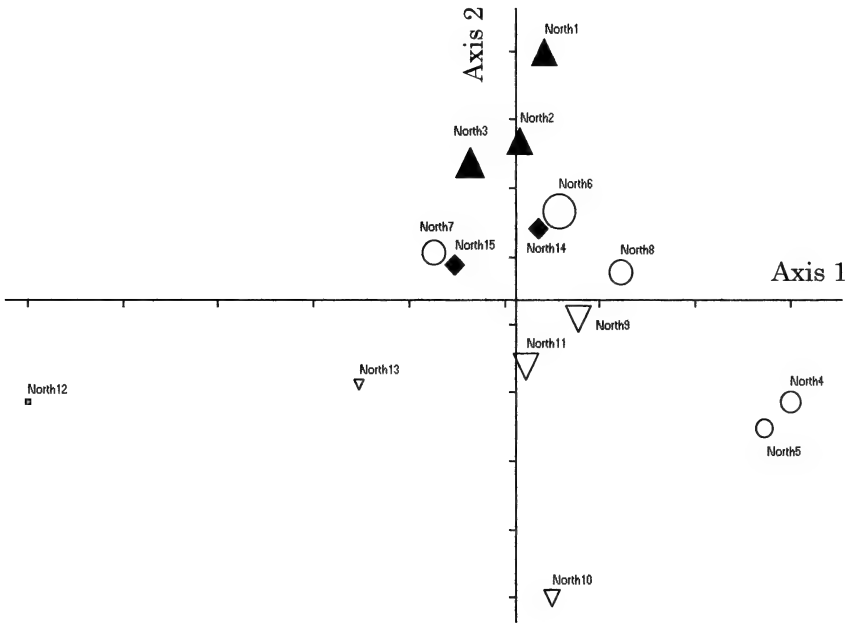


FIG. 4. A Bray-Curtis ordination using Sorenson similarity coefficients showing patterns for 15 foxtail pine stands from the Klamath Mountains. Symbols are proportional to foxtail pine importance. Marble Mountains (closed diamonds), Russian Peak (open triangles), Trinity Alps (open circles), Trinity Mountains (open squares), and Yolla Bolly Mountains (closed triangles).

TABLE 4. CHARACTERISTICS OF 15 FOXTAIL PINE STANDS IN THE SOUTHERN SIERRA NEVADA. Density given in trees/hectare, basal area in m<sup>2</sup>/hectare, and relative values in percent. Data are from Vankat (1970) and Ryerson (1983). Averages  $\pm 1$  SE in parentheses.

Stand	Vankat		Ryerson		
	Density	Basal area	Density	Basal area	Foxtail pine importance
1	500	220	78	38	276
2	0	0	193	9	296
3	500	161	34	13	122
4	300	182	178	36	120
5	600	67	54	6	68
6	400	66	52	18	90
7	200	97	74	17	59
8	600	n/a	74	35	75
9	200	151	273	61	212
10	—	—	222	75	285
11	—	—	11	2	16
12	—	—	61	26	273
13	—	—	111	4	44
14	—	—	29	4	55
15	—	—	51	15	181
Average	367 (69)	118 (24)	100 (20)	24 (6)	145 (26)

to 56 m<sup>2</sup>/ha (Table 4). Stand elevations ranged from 2900 m to 3650 m. Importance values for foxtail pine were at or approached 300 with western white pine, whitebark pine, and lodgepole pine as minor stand components. This prompted Vankat to identify a foxtail pine forest type. Tree ring counts indicated that foxtail pine cover and density began increasing approximately 110 years ago in accordance with decreased grazing levels by sheep.

*Interregional comparison.* A comparison to Ryerson's data set showed that stand basal area, foxtail pine basal area, elevation, and conifer richness differed between regions, but importance values did not (Table 5). A comparison to Vankat's data set showed that stand density, foxtail pine density, and foxtail pine relative basal area differed between regions (Table 5). Variances around these estimates also differed between regions, with the southern Sierra Nevada having significantly greater variance estimates (Table 5). Comparisons between Ryerson's and Vankat's data sets showed differences in stand density, foxtail pine relative density, and foxtail pine relative basal area (Table 5).

The Bray-Curtis ordination using all stands did not cluster stands exclusively by region (Fig. 5), but there was broad separation of the majority of Klamath Mountain stands from a bifurcated grouping of southern Sierra Nevada stands dependent upon dominance of either foxtail or whitebark pine (Fig. 5). The stands with the highest importance values for foxtail pine were exclusively identified in the Sierra. Axis I in the ordination using all stands was highly correlated with foxtail pine importance ( $R = 0.855$ ) and axis II with whitebark pine importance ( $R = -0.833$ ). These axes had relatively high explanatory power ( $R^2 = 0.757$ ). Four major clusters were identified: 1) stands dominated by foxtail

pine, 2) stands with foxtail pine and whitebark pine, 3) stands with foxtail pine and red fir, and 4) mixed stands with foxtail pine, red fir, and western white pine (Fig. 5).

Stands with red fir and western white pine were associated with the lower elevations, while stands with whitebark pine were associated with higher elevations or northern stands. Incense-cedar, Douglas-fir, and mountain hemlock were sampled only within the Klamath Mountains, while limber pine and mountain juniper (*Juniperus occidentalis* Hook.) were exclusively present in the Sierra Nevada. Red fir was present in the Sierra as the typical variety (*Abies magnifica* var. *magnifica*) and in the Klamath by Shasta red fir (*Abies magnifica* Andr. Murray var. *shastensis* Lemmon). An inverse relationship between foxtail pine importance and conifer species richness was evident in the results of both procedures (Figs. 4, 6).

DISCUSSION

Recent genetic research has documented inter-regional and intraregional divergences of foxtail pine populations (Oline et al. 2000). We expected similar conclusions when compositionally comparing stands at these levels. Therefore we expected foxtail pine stands in close proximity within the Klamath Mountains to be similar, especially if they were located on the same substrate. Likewise, we expected the Klamath Mountains and southern Sierra Nevada stands to differ in several ways.

Both regions had simple stands dominated by foxtail pine, but this organization was found more often in the southern Sierra Nevada. Mixed stands with red fir or whitebark pine cut across regions. As found here, past studies suggested the lack of ecological differences between stands with different

TABLE 5. STAND AND FOXTAIL PINE CHARACTERISTICS COMPARED USING TWO-SAMPLE T-TESTS (T), MANN-WHITNEY U TESTS (Z), AND HARTLEY'S EQUAL VARIANCE TESTS BETWEEN KLAMATH AND SIERRA REGIONS. Comparison to Ryerson (1983) is indicated by R and to Vankat (1970) by V. Equal variance tests were not conducted on non-normal data.

Variable	Source	Two-sample T and Mann-Whitney U tests			Hartley's test	
		Sample sizes	Critical value	P-value	F-value	P-value
Conifer richness	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = 3.543**	0.00141**	1.600	0.389848
Elevation (m)	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	Z = 4.668**	0.000003**	—	—
Importance value	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = -0.814	0.424904	4.026**	0.013294
Basal area	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = 1.847***	0.08583***	248.941**	0.000001
Density	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = 0.248	0.806775	264.552**	0.000001
Relative basal area	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	Z = -0.560	0.575511	—	—
Relative basal area*	V	n <sub>1</sub> = 15 n <sub>V</sub> = 9	Z = 2.930**	0.003388**	—	—
Relative density	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	Z = -0.477	0.63325	—	—
Relative density*	V	n <sub>1</sub> = 15 n <sub>V</sub> = 9	Z = 3.171**	0.001521**	—	—
Relative frequency	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = -1.135	0.27096	5.817**	0.002213
Stand basal area	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = 2.310**	0.036552**	264.552**	0.000001
Stand density	R	n <sub>1</sub> = 15 n <sub>R</sub> = 15	T = 0.848	0.405853	3.373**	0.029873
Stand density*	V	n <sub>1</sub> = 15 n <sub>V</sub> = 9	T = -3.653**	0.004152**	4.039**	0.037774

\* Tests for statistical differences between these values from Ryerson (1983) and Vankat (1970) were significant with  $\alpha = 0.05$ . \*\* Significant at  $\alpha = 0.05$ . \*\*\* Significant at  $\alpha = 0.10$ .

red fir varieties (Barbour and Woodward 1985). Mixed foxtail pine stands with western white pine grew on sites with similar conditions to those for unmixed stands in both regions suggesting similar habitat needs by both species within and between regions. This result was expected because of western white pine's prevalence in many subalpine forest types within the Californian mountains (Sawyer and Keeler-Wolf 1995). As expected there were species exclusive to each region (Griffin and Critchfield 1972), but they were not important in differentiating stands at the regional level.

Ryerson found that mixed stands with whitebark pine were associated with less-developed soils at higher elevations typical of xeric, nutrient-limited sites, while mixed stands containing red fir were associated with deeper and more developed soils typical of mesic, nutrient-rich sites. Our analyses identified a cluster of foxtail pine-red fir dominated stands that cut across both regions. Within the Klamath Mountains, red fir was a more common associate of species rich stands, but these were neither more mesic nor nutrient-rich than stands dominated by foxtail pine. Stands dominated almost exclusively by foxtail pine in the Klamath Mountains were typically found on sites intermediate to the

extremes mentioned by Ryerson, on ultramafic soils, or homogeneous substrate compositions.

An alternate explanation to Ryerson's site limitation hypothesis may better explain the foxtail pine stands mixed with red fir. These stands may be the product of species-specific elevation limits. Within the Sierra Nevada, conifer species zone over a considerable elevation range. Much of the upper montane red fir forests are replaced with lodgepole pine and whitebark pine forests as elevation increases (Potter 1998). Individual red fir trees are found in these types illustrating broad ecotones between forest types. This is not the case in the compressed forest zones found in the Klamath Mountains.

The comparison of Ryerson's and Vankat's data sets illustrated important differences suggesting that different sampling methods accounted for the differing estimates of basal area. Stand selection criteria may have been even more important. Ryerson picked stands at marginal locations, while Vankat chose stands in areas with extensive foxtail pine dominance. The marginal stands of Ryerson were expected to have high variances if foxtail pine stands exhibited a core-periphery spatial structure. Comparisons revealed that Ryerson's estimates were more variable and could be attributed to sampling from different core and peripheral populations.

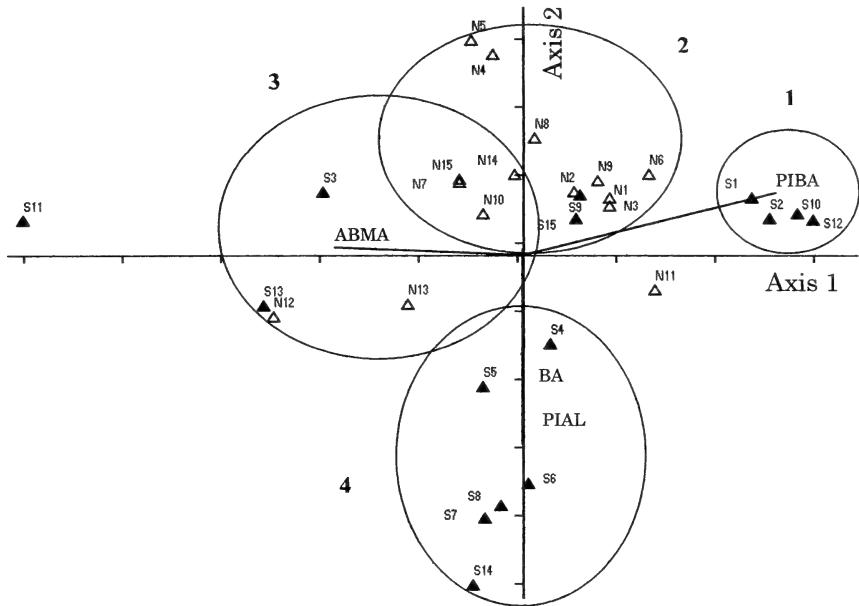


FIG. 5. A Bray-Curtis ordination using Sorenson similarity coefficients showing patterns for 30 foxtail pine stands in the Klamath Mountains and southern Sierra Nevada. Open circles represent the Klamath Mountains stands. Closed triangles represent the southern Sierra Nevada stands. 1) stands dominated by foxtail pine, 2) stands with foxtail pine and whitebark pine, 3) stands with foxtail pine and red fir, and 4) mixed stands with foxtail pine, red fir, and western white pine. ABMA = red fir density, BA = stand basal area, PIAL = whitebark pine density, PIBA = foxtail pine density.

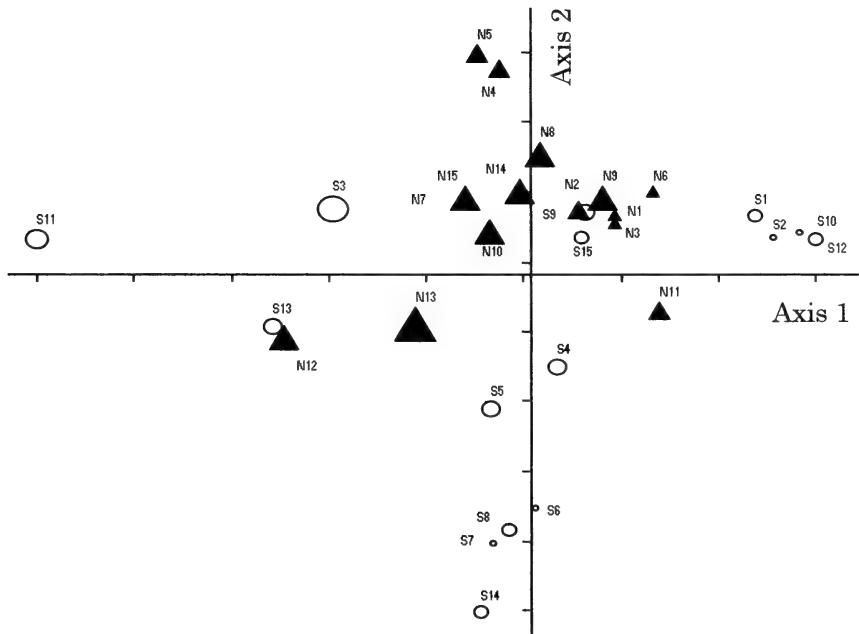


FIG. 6. A Bray-Curtis ordination using Sorenson similarity coefficients showing patterns for 30 foxtail pine stands in the Klamath Mountains and southern Sierra Nevada. Open circles represent the Klamath Mountains stands. Closed triangles represent the southern Sierra Nevada stands. Symbol sizes are proportional to the conifer species richness found within each stand.

The finding that called most for an interpretation was the inverse relationship between foxtail pine importance and conifer diversity prominent in the Klamath Mountains. Because conifer diversity was also correlated to substrate heterogeneity, simple causal explanations are difficult. Several authors have an explanation for this pattern that might be called the marginal hypothesis (Wright and Mooney 1965; Ryerson 1983; Sawyer and Thornburgh 1988; Kruckeberg 1992; Oline et al. 2000). They offer that within marginal habitats decreased biotic interactions lead to increased species diversity. Marginal habitats have been hypothesized as composed of nutrient limited soils (Sawyer and Thornburgh 1988; Kruckeberg 1992; Oline et al. 2000), extreme climate (Ryerson 1983), and cyclically disturbed habitat (Murray et al. 2000). Two possible marginal site types exist within the distributional limits of foxtail pine—high elevation sites and ultramafic soils.

Ryerson proposed that the highest elevation stands within the Sierra Nevada simulated marginal habitat, but foxtail pine acts as a timberline species in the center of its range when south of whitebark pine's range (Scuderi 1987). These stands are simple with one or two species, rather than mixed as proposed by the marginal hypothesis. This may be a function of species distribution ranges along the Sierran crest. Similar elevations are absent in the Klamath Mountains, and elevation was not correlated to species richness.

Ultramafic soils have been argued as marginal sites that isolate species and promote increased diversity. This soil type is absent within the range of foxtail pine within the southern Sierra Nevada. Stands located on marginal ultramafic soils in this study were not more diverse than stands located at better sites (see Fig. 2). Nor were they less diverse with respect to conifer diversity. Stands with high conifer diversity were found on schists, gabbro, and peridotite in the Yolla Bolly Mountains, Trinity Alps, and Trinity Mountains, as were the stands dominated by foxtail pine. The most diverse stand, sampled at Russian Peak, was on glaciated granite. These results suggest that ultramafic soils do not directly control conifer species diversity as proposed in the marginal hypothesis. Nor do they control foxtail pine importance (see Fig. 2).

Conifer diversity in the Klamath Mountains was variable, and was greatest in the northern-most stands. The stands in the Yolla Bolly Mountains were well south of the range of lodgepole pine and whitebark pine and at the range limits for mountain hemlock and western white pine, reducing the species pool in the south. In the northern stands, these subalpine species mixed with montane conifers such as Douglas-fir, incense-cedar, and white fir. Within the Sierra Nevada, the limits of these montane species are well below that of foxtail pine.

Analysis of Jaccard similarity coefficients by sub-region revealed that foxtail pine stands in close

proximity were more similar to one another than to stands in distant sub-regions. This pattern indicated an island-like distribution of foxtail pine and other species as predicted by the mountain island effect hypothesis (Brown 1971; Hamrick et al. 1994). This hypothesis argues that mountain tops are isolated collections of species experiencing ecological processes commonly observed within insular systems. These patterns may be the result of slow dispersal rates inherent to conifers and/or historical climate fluctuations. Mohr's et al. (2000) recreation of post-glacial vegetation history at two lakes in the Trinity Mountains supports this possibility. The vegetation patterns and histories differed as much as they were similar even though these lakes are approximately 4.5 km apart.

Inferences with our data suggest that the mountain island effect enhanced by substrate heterogeneity better explains conifer species diversity patterns than does the marginal hypothesis. Substrate heterogeneity was positively correlated with conifer diversity and glaciated substrates. Rocky conditions such as moraines would isolate individual trees in favorable microsites if the species was in the area to take advantage of these sites. The high diversity stand at Crater Lake was partially logged and it had high diversity. Qualitative observations suggested that boulders isolated the new seedlings and saplings establishing after the disturbance.

#### SUMMARY

Foxtail pine stands within the Klamath Mountains and southern Sierra Nevada did not differ dramatically in structure. Foxtail pine importance was constant across both regions, but species richness, stand basal area, and elevation differed between regions. Within the Klamath Mountains, conifer diversity, foxtail pine relative density, and substrate heterogeneity differed among five sub-regions. Conifer diversity and foxtail pine importance were not correlated to substrate type (e.g., ultramafic soils) as previously hypothesized. Significant correlations were observed among foxtail pine importance, conifer diversity, and substrate heterogeneity. These correlations were more significant on glaciated substrates versus unglaciated substrates. Inferences from our data suggest that foxtail pine importance and conifer diversity in the Klamath Mountains may be regulated by a mountain island effect enhanced through substrate heterogeneity, but more research is needed to tease apart the causal mechanisms within these correlations.

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tires obtained on the back roads of Siskiyou, Trinity, and Tehema counties.

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## REVIEW

*The manzanitas of California, also of Mexico and the world*, by Phillip V. Wells. 2000. Published by P. V. Wells, Department of Ecology and Evolutionary Biology, Haworth Hall, University of Kansas, Lawrence KS 66045. Available from Cody's Books, Berkeley, CA for \$53.00. ISBN: 0-933994-22-2.

The recent review of *Trees and Shrubs of California* (Stuart and Sawyer 2001) by Rejmánek (2001) underscores the need for a review of *The manzanitas of California* (Wells 2000). Rejmanek points out that there are “more than 40 excluded species of *Arctostaphylos*” in Stuart and Sawyer (2001) and he suggests that people would be better off getting Wells (2000) if they have an interest in this quintessentially Californian group of woody shrubs. To a degree, we agree—but with some important caveats that should be kept in mind.

P. V. Wells has made the study of manzanitas a lifetime work and this self-published, un-peer reviewed book demonstrates both the best and the worst of this kind of situation. Most of the information in the book, for example, can be found in previous publications of his, including most of the figures (see, e.g., Ecological Monographs 32:79–103 [1962], Evolution 23:264–267 [1969], The Four Seasons 7:17–21 [1987], 8:46–70 [1990], 9: 64–69 [1992]). Wells published his treatment on *Arctostaphylos* in the 1993 Jepson Manual (Hickman 1993) (Chapter V). He also published a phylogenetic hypothesis for *Arctostaphylos* in 1992 (Chapter IV) (Wells 1992) in which he divides the genus into two subgenera and six sections. This latest book presents this treatment in detail and ignores later publications that cast serious doubt on Wells' phylogenetic hypothesis (Markos et al. 1998). He then goes on to trivialize important new findings in the genus by Keeley and his students (Keeley 1994; Keeley et al. 1997a, b). Figures in this book come from the original publications and many of the species names are woefully out of date, no longer valid even in the treatment by Wells. In Chapter V, he includes small, fuzzy, black and white photos of herbarium specimens to illustrate species; none of these are sharp enough or show the appropriate characters to be of much use. While he provides some interesting discussions, for example, concerning reticulate evolution, Wells has not published data that would enable objective evaluation of his conclusions, nor does it exist as a table or appendix in this book. The overall impression is that Wells has decreed an ideal manzanita world that he can perceive and which now has been formally revealed. Indeed, but if only those plants in the field would behave!

With these *minor* criticisms aside, we acknowledge that the majority of the taxa recognized by Wells are probably distinct lineages and this volume provides a wealth of information about them. Indeed, we agree with Wells that manzanitas are the most diverse and fascinating genus of woody shrubs in the California Floristic Province (one of 25 global “hotspots” on the planet [Mittermeier et al. 2000]). Most importantly, this book distills Wells' long years of scholarly research into the genus and provides an invaluable resource for any serious manzanita student. As mentioned above, Wells develops an intriguing chapter on reticulate evolution in *Arctostaphylos* (Chapter VII). This informative discussion concerning hybridization and speciation in manzanitas articulates his hypothesis concerning diploid hybridization. Wells presents scatter diagrams and multivariate-analytic figures that suggest evidence of hybrid origin between species such as *A. canescens* and *A. andersonii* (leading to intermediate species such as *A. glutinosa* and *A. auriculata*). Unfortunately, the data supporting these studies is missing, and in tables speculating on species of possible hybrid origin, the inclusion of many plausible parents (e.g., *A. glutinosa* from *A. canescens* × *A. andersonii*) are undermined by a number of frankly preposterous suggestions (e.g., *A. pilosula* from *A. wellsii* × *A. glauca*).

Wells also provides a lot of practical material. He gives interesting regional keys to manzanitas in Chapter VI, a chapter rich in historical lore. The Introduction contains a discussion of generic relationships between *Arctostaphylos* and other members of the Arbutioideae (Arbutaeae) distilled from Diggs and Breckon (1981) through Wells' own perspective. Hileman et al. (2001) provide a molecular counterpoint that reinforces the general accuracy of the generic circumscriptions that Wells describes for this monophyletic group.

The Character Analysis (Chapter II) of *Arctostaphylos* illustrates the fundamental flaw in Wells' classification system. He lists 70 morphological traits that he claims he has analyzed for 61 species. He then describes character states for these traits and goes on to fashion elaborate descriptions of species that are infinitely complex based upon this enormous data set (again, which is not tabulated in the book). These species descriptions are enumerated in Chapter IV and ordered into the same phylogenetic scheme that Wells (1992) proposed eight years ago. The flaw is that manzanitas don't obey the world according to P. V. Wells, as was illustrated by Keeley (1994), Markos et al. (1998), Vasey and Parker (1999), and our extensive field observations. Wells continues with the belief that panicles can be described as racemes (with up to 7



branches!), and that nascent inflorescences with variable bract characters (leafy vs. scaly bracts) can be classified as either one state or the other exclusively. As a consequence, we have found that a great deal of confusion and mystification is created by a treatment that tends to elicit more frustration than enlightenment.

And so, we caution, if you buy this book, focus on the real entities and not necessarily on the bi- or trinomial classification system offered by Wells. Luxuriate in the lore but take lightly the conclusions. Particularly, defer judgments regarding phylogenetic relationships until an alternative and probably molecular phylogeny is worked out that meshes with morphology, cytology, and ecological information and that will also employ a more contemporary species concept. There is a rich literature on manzanitas by some great California botanists and evolutionary biologists (e.g., Eastwood [1934], Jepson [1922], Dobzhansky [1953], Stebbins and Major [1965], etc.). These scientists recognized the extraordinary importance of *Arctostaphylos* to understanding driving forces in the evolution of California's remarkable flora. Wells' book culminates a wild and woolly era in the history of manzanita taxonomy that diverged from this venerable tradition. Will Wells (2000) be the last word on manzanitas? We don't think so (Keeley 1998; Keeley et al. 1994, 1997a, b; Markos et al. 1998; Vasey and Parker 1999; Hileman et al. 2001).

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*Illustrated field guide to selected rare plants of northern California.* Edited by Gary Nakamura and Julie Kierstead Nelson. 2001. University of California Agriculture and Natural Resources Publication 3395, Oakland, CA. 370 pp. Softcover \$36.00. ISBN 1-879906-5470.

For those interested in the botany of northern California, this field guide is a real treat. This book richly illustrates and describes 149 of the rarer plant taxa found in northern 10 counties in the state (Butte, Del Norte, Glenn, Humboldt, Lassen, Modoc, Plumas, Shasta, Siskiyou, and Trinity Counties). The authors focus mainly on plants presumed extinct or rare in California, Lists 1A and 1B respectively in the 6th edition CNPS Inventory (CNPS 2001). Also included are six List 2 (rare in California, but more common elsewhere), one on List 3 (review list), and four on List 4 (watch list). The 149 taxa include three that are state-listed as endangered, 12 that are state-listed as rare, eight that are federally-listed as endangered, and three that are federally listed as threatened.

It is easy to jump over the first 40 pages of introduction to enjoy the species descriptions. Each is a two page treatment. The spiral binding allows for quick access. Plants are arranged alphabetically by genus, with the name in the upper left and lower right corners to make it easy to find a plant. Each treatment involves a large photograph of a mature plant, a small photograph of its habitat, and a map indicating occurrences by USGS quadrangle location.

On the facing page, a line art illustration accompanies a description of the plant, habitat, and location. Scientific names follow the new edition of the CNPS Inventory, as do synonymy, common name(s), family names, distribution, elevation, and quadrangle codes. Habitat designations generally follow those in the CNPS Inventory, but in some cases, the habitat descriptions are broader. In the Key Feature section, the first paragraph typically describes the plant. The second paragraph discusses similar taxa, and, if necessary, instructs the reader to "consult an expert to verify identification." If this is the case, a list of diagnostic features accompanies an expert symbol. Flowering times and identification times, which may differ if fruits are required, finish the presentation. Illustrations are drawn from 26 sources including lovely, original art by Linda Vorobik.

The book has no keys, exhaustive descriptions, or complete synonymy. It assumes a basic knowl-

edge of plant identification and is not intended to substitute for standard botanical references or field guides. Instead, the book's purposes are to "... help the reader develop an accurate search image ..." and to "... learn how to accurately distinguish rare plants from similar species in the field ..." The editors involved 28 contributors, who make up the Northern California Botanists, an *ad hoc* committee of federal, state, and consulting botanists. More than other botanists, they are faced each field season with a new set of recruits to conduct plant surveys. This book is designed for them, but it will be useful to seasoned botanists as well.

Turning to the introduction, the reader finds the expected definitions, a short description of state and federal laws concerning protecting and conserving plants, and an explanation of how to use guide. Next come two extensive tables. The first lists species by geographic subdivisions of the state found in The Jepson Manual (Hickman 1993). The second table lists species by habitat in each region.

These tables are enlightening. As expected, rare plants along the coast were most common on the dunes, but the north coast conifer forest is not far behind. I expected to find a spate of serpentine species in the Klamath and North Coast Ranges, but not necessarily in mid-elevation forests and woodlands. The same conclusion came from reviewing the lists for the Cascades, Sierra Nevada, and the Great Basin. The point was made most vividly when I saw the habitats of *Cryptantha crinita* and *Lotus rubriflorus*. The traveler on Interstate 5 drives by miles of similar looking dry streams and grasslands. This book will help people get over the idea that all rare plants only grow in special places. With this book in hand and its great photographs, people can shed that misconception, as well as develop accurate search images for northern California's rare plants.

I doubt that you will find the book in most bookstores, but it can be ordered from the University of California, Agriculture and Natural Resources (ANR) Catalog at <http://anrcatalog.ucdavis.edu/>

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## NOTEWORTHY BRYOPHYTE RECORDS FROM THE MOJAVE DESERT

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### ABSTRACT

Significant range expansions in the northern Mojave Desert are documented for twenty-three species of bryophytes, nine of which are new to the region. *Barbula convoluta*, *Claopodium whippleanum*, *Entosthodon planoconvexus*, *Fissidens sublimbatus*, *Grimmia americana*, *Reboulia hemispherica*, *Syntrichia bartramii*, *Weissia condensa*, and *Asterella californica* are new to the flora of Nevada.

The northern Mojave Desert encompasses four counties: Clark and Nye Cos., Nevada, Washington Co., Utah, and Mohave Co., Arizona (MacMahon and Wagner 1985). Recently, a list of bryophyte species from this region was compiled from the literature (Stark and Whittemore 2000), drawing chiefly from state and regional checklists and treatments (Lawton 1958; Haring 1961; Flowers 1973; Spence 1988). The bryophyte flora of the region consists of 75 species of mosses and 5 species of liverworts. More than half of the bryophytes from the northern Mojave Desert belong to the more xeric families Pottiaceae, Grimmiaceae, and Orthotrichaceae.

Ongoing collecting efforts in southern Nevada indicate that this region is not well explored bryologically, and this applies to the entire state (Heise 2000). The recent discovery of a new species of *Didymodon* in the remote southeastern portion of Nevada (Zander et al. 1995), and an as yet undescribed species in the liverwort genus *Targionia* that appears to be endemic to the Mojave Desert (Whittemore 1996) indicate exploration is needed. In the present paper, we discuss several species of bryophytes that are reported new to the northern Mojave Desert, or whose distributions are considerably broadened within the region. Nomenclature follows Anderson et al. (1990), Zander (1993), and Stotler and Crandall-Stotler (1977).

### BRYOPHYTA

#### *Barbula convoluta* Hedw.

Nevada, Clark Co., southern Gale Hills, lower end of Lovell Wash, 0.3 km upstream of confluence

of Lovell Wash and West End Wash, along steep, north-facing outcrop adjacent to dirt road, elev. 550 m, *Stark NV-1941* (UNLV), 1942 (UNLV, BUF). Nevada state record. This is the first report of this rather wide-ranging species from the Mojave Desert, with the only other report from the interior basins of North America (southern Idaho, Flowers 1973; Spence 1988). From western North America, *B. convoluta* is known from British Columbia to Baja California (Lawton 1971; Zander 1994a).

#### *Claopodium whippleanum* (Sull. in Whipple & Ives) Ren. & Card.

Nevada, Clark Co., Spring Mountains, Red Rock Canyon National Recreation Area, steep side canyon near mouth of Red Rock Canyon, near confluence with Red Rock Wash; in deep shade beneath boulders, on sandstone rock and dead wood, elev. 1450 m, *Stark NV-316* (UNLV). Nevada state record. Found in an area that never receives direct sunlight, in a side canyon on a steep slope under boulders. In North America, the species ranges from northwestern Mexico to British Columbia (Crum and Buck 1994), and is reported from southern California as occasional in cismontane lowlands (Hartill et al. 1979). It is distributed in western North America and also the Mediterranean region (Schofield and Crum 1972). A disjunct population was reported from high elevation in northeastern Arizona (Apache Co., 9500 ft, Haring 1961).

#### *Coscinodon calyptratus* (Hook. in Drumm.) C. Jens. ex Kindb.

Reported from the Mojave Desert of southwestern Utah (Hastings 1999). Previously reported from Mohave County, Arizona (Haring 1961, as *Grimmia calyptrata* Hook.), and from Lincoln Co., Ne-

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vada (Lawton 1958, as *Grimmia calyptrata* Hook.). This species is broadly distributed in Nevada and Utah, reaching its southwesternmost extent in the Mojave Desert (Hastings 1999).

*Crossidium seriatum* Crum & Steere

Nevada, Clark County, northern foothills of Lime Ridge, ca. 16 km north of Gold Butte, elev. 487 m, *Stark NV-232a* (UNLV, MEXU); southern Moapa Valley, sandstone bluffs along periphery of valley, ca. 8 km south of Overton, along Hwy 169, elev. 488 m, *Stark NV-872* (UNLV, MEXU); Black Mountains, Lake Mead National Recreation Area, gypsum formation 2.1 km down Boathouse Cove Road from North Shore Road turnoff, elev. 650 m, *Stark & Bonine NV-3045* (UNLV); Arizona, Mohave County, Lake Mead National Recreation Area, Lake Mead Landing, mouth of Kingman Wash, elev. 396 m, *W. Niles* s.n., 24 Feb 1995 (UNLV). Recently recorded from the state of Nevada (Zander et al. 1995), the range of *C. seriatum* is expanded to a scattering of southern Nevada locations and also into Mohave County, Arizona. This globally rare species is presently known from only a handful of populations worldwide outside of the state of Nevada: Mariposa County, Arizona (Zander 1977), Cedros Island, Mexico, San Diego County, California (Stark and Whittemore 1992), and Spain (Cano et al. 1992).

*Didymodon vinealis* (Brid.) Zand.

Nevada, Clark County, Southern Gale Hills, lower end of Lovell Wash, 0.3 km upstream of confluence of Lovell Wash and West End Wash, along steep, north-facing outcrop adjacent to dirt road, elev. 550 m, *Stark NV-1946* (UNLV); Lake Mead National Recreation Area, 4.3 km south of Rogers Spring, narrow canyon on north side of North Shore Rd, elev. 750 m, *Stark NV-2059a* (UNLV); Newberry Mountains, Lake Mead National Recreation Area, "Needles Eye", ca. 7.2 km north on Christmas Tree Pass Rd from Hwy 77E, elev. 817 m, *Stark NV-76* (UNLV). Recently reported from the northern Mojave from the River Mountains as an incidental species (Stark 1997), the range of *D. vinealis* is considerably broadened here.

*Entosthodon planoconvexus* (Bartr.) Grout

Nevada, Nye County, Nevada Test Site, Rock Valley, north-facing foothills of Spectre Range, elev. 1159 m, growing with an undescribed species of *Targionia*, *Stark NV-724* (UNLV). Nevada state record, and one of only four localities worldwide. Other known localities include Washington County, Utah (Flowers 1973), Pima County, Arizona (Haring 1961), and the northern Egyptian desert (Shabbara 1999). The specimen cited herein (*Stark NV-724*) differs from descriptions of *E. planoconvexus* in having a pale (not red) seta, a relatively narrow capsule that is strongly contracted under the mouth

when dry, and a rudimentary peristome. The latter features align it with *E. tucsonii* (Bartr.) Grout. However, *E. tucsonii* has spores twice as large as *Stark NV-724*, making this determination improbable. Clearly, a revision of North American *Entosthodon* is needed.

*Fissidens sublimbatus* Grout

Nevada, Clark County, Newberry Mountains, Lake Mead National Recreation Area, Pipe Spring Canyon, near Pipe Spring, west-facing soil in rock crevice, elev. 732 m, *Stark NV-99* (UNLV, PAC). New to the northern Mojave Desert and a Nevada state record. Known also from Arizona, California, New Mexico, and Baja California (Pursell 1994).

*Funaria hygrometrica* Hedw.

Nevada, Clark County, Newberry Mountains, Lake Mead National Recreation Area, "Needles Eye," ca. 7.2 km north on Christmas Tree Pass Rd from Hwy 77E, elev. 817 m, *Stark NV-80* (UNLV); Virgin Mountains, east base of South Virgin Peak Ridge, Lime Spring Canyon, abundant in moist drainages, *W. Niles* s.n., 22 Mar 1996 (UNLV). This cosmopolitan species is reported as new to southern Nevada, having previously been reported from Mohave County, Arizona (Haring 1961).

*Funaria muhlenbergii* Turn.

Nevada, Clark County, northern River Mountains, Lake Mead National Recreation Area, 5.6 km due east of Saddle Island, elev. 610 m, *Stark NV-144* (UNLV); Eldorado Mountains, Keyhole Canyon Archeological Site, just north of base of Keyhole Canyon, elev. 274 m, *Stark NV-190b* (UNLV); Muddy Mountains, southern end of White Basin, adjacent to West Longwell Ridge, ca. 6.4 km by road northwest of Bitter Spring, elev. 650 m, *Stark & Bonine NV-3013* (UNLV). Reported from the California Mojave (Harthill et al. 1979), and broadly distributed in western North America (Smith 1994).

*Grimmia americana* Bartr.

Nevada, Clark County, Newberry Mountains, Lake Mead National Recreation Area, Grapevine Canyon, on north-facing rock, elev. 793 m, *Stark NV-16* (UNLV). Nevada State record, and one of only three populations of this species known worldwide, one from Arizona (Pima Co., Crum 1994), and one from western Texas (type locality, Jeff Davis County, Texas; Crum and Anderson 1981). This species is not listed in Haring (1961) as occurring in Arizona, and is not yet known from Mexico (Crum 1994). *Grimmia americana* has bistratose upper leaf cells, which distinguish it from *G. plagiopodia* Hedw., and is peristomate, which distinguishes it from *G. anodon* Bruch & Schimp. in B.S.G. *Grimmia plagiopodia* is listed in Haring

(1961) as occurring only in Yavapai County, Arizona, from two collections, while *G. anodon* is widespread in the southwestern U.S. (Lavin 1982).

*Grimmia moxleyi* Williams in Holz.

Nevada, Clark County, Muddy Mountains, southern end of White Basin, adjacent to West Longwell Ridge, ca. 6.4 km by road northwest of Bitter Spring, elev. 650 m, *Stark & Bonine NV-3004* (UNLV); foothills of Black Mountains, Lake Mead National Recreation Area, along tributary to Manganese Wash (from the northwest), ca. 6.4 km north of Boathouse Cove, elev. 650 m, *Stark & Bonine NV-3071* (UNLV). New to the northern Mojave Desert exclusive of California. *Grimmia moxleyi* is reported from the California Mojave Desert as infrequent (Harthill et al. 1979), and its presence is expected based on a Death Valley locality noted in Koch (1954). A common associate of *G. orbicularis* Bruch ex Wils. in Nevada, *G. moxleyi* is endemic to the southwestern U.S. and adjacent northern Mexico (Greven 1999). It has been reported without specifics from Arizona and Nevada (Crum 1994). Recently, Muñoz (2000) regarded *G. moxleyi* as synonymous with the wide-ranging *G. orbicularis*, indicating ample variability in hair-point development among southwestern populations.

*Homalothecium nevadense* (Lesq.) Ren. & Card.

Nevada, Nye County, Spring Mountains, Wood Canyon, in vicinity of Wood Canyon Spring, *Stark & Landau NV-1794* (UNLV). First report for the Mojave Desert. This species is reported from southern California (Harthill et al. 1979) as frequent in the region, but excluding deserts. The species reaches its southernmost extent in northern Arizona (Flowers 1973).

*Hypnum vaucheri* Lesq.

Nevada, Clark County, Spring Mountains, Red Rock Canyon National Recreation Area, steep side canyon near mouth of Red Rock Canyon, near confluence with Red Rock Wash, on shaded rock, elev. 1450 m, *Stark NV-315b* (UNLV). New to the Mojave Desert. Frequent in southern Utah along the Colorado-Green River Basin (Flowers 1973).

*Microbryum starkeanum* (Hedw.) Zand.

Nevada, Clark County, lower end of Borax Wash, southern Gale Hills, *Stark NV-1944* (UNLV). New to the Mojave Desert. Guerra and Cano (2000) prefer to retain this species in *Pottia*, as *Pottia starkeana* (Hedw.) Müll., because of its stegocarpous sporophyte.

*Pseudocrossidium crinitum* (Schultz) Zand.

Nevada, Clark County, Muddy Mountains, Valley of Fire State Park, 0.5 km south of "Mouse's

Tank," sandstone bluffs on west side of road, elevation 700 m, *Stark & Bonine NV-3076, 3084* (UNLV). Second report for state of Nevada. The locality cited may be the same populations noted by Lawton (1958, as *Tortula aurea* Bartt.). This report thus confirms the only known population from the Mojave Desert, with the nearest known locality just outside the Mojave Desert in southern Utah (Spence 1987). This species is fairly common in Mexico, according to Zander (1994b), occurring in several Mexican states, and is listed from five counties in Arizona (Haring 1961). Despite the abundance of *P. crinitum* at this site, no sporophytes were found, consistent with the pattern of an absence of male plants in North America.

*Pterygoneurum subsessile* (Brid.) Jur.

Nevada, Clark County, Eldorado Mountains, Keyhole Canyon Archeological Site, just north of base of Keyhole Canyon, elev. 274 m, *Stark NV-192a* (UNLV); Newberry Mountains, Lake Mead National Recreation Area, Grapevine Canyon, 3.2 km north on Christmas Tree Pass Rd from Hwy 77E, beyond petroglyphs to the east, elev. 854 m, *Stark NV-22c* (UNLV). Second report from the northern Mojave Desert; found previously in Washington County, Utah (Flowers 1973).

*Syntrichia bartramii* (Steere in Grout) Zand.

Nevada, Clark County, Newberry Mountains, Lake Mead National Recreation Area, Grapevine Canyon, 3.2 km north on Christmas Tree Pass Rd from Hwy 77E, beyond petroglyphs to the east, elev. 854 m, *Stark NV-32B, 38B* (UNLV). Nevada state record. Previously reported from the southern Californian Mojave Desert (Harthill et al. 1979), *S. bartramii* occurs in northwestern Mexico and in the bordering states of Arizona, New Mexico, and Texas, with infrequent reports north of this region (Mishler 1994). One of the two specimens cited above from Nevada was found on juniper growing with *S. pagorum*, noteworthy in that epiphytic mosses are exceedingly rare in the Mojave Desert below 2000 m. Variation in this species is complex and should be studied in association with plants occurring in southern California, where it is possible that an undescribed species is present.

*Syntrichia pagorum* (Milde) Amann

Nevada, Clark County, Newberry Mountains, Lake Mead National Recreation Area, "Needles Eye," ca. 7.2 km north on Christmas Tree Pass Rd from Hwy 77E, elev. 817 m, *Stark NV-82A* (UNLV); Pipe Spring Canyon, in vicinity of Pipe Spring, elev. 732 m, *Stark NV-91* (UNLV). New to the Mojave Desert. Previously reported from Nevada (Crum and Anderson 1981), this species is distributed from eastern North America across the southern portion of the USA to the west coast. However, reports are lacking for Utah and southern

California. *Syntrichia pagorum* is known only from female plants in the USA.

*Syntrichia princeps* (De Not.) Mitt.

Nevada, Clark County, Spring Mountains, Red Rock Canyon National Recreation Area, near mouth of Red Rock Canyon, near confluence with Red Rock Wash, on partially shaded rock, elev. 1450 m, *Stark NV-291* (UNLV); Virgin Mountains, east base of South Virgin Peak Ridge, Lime Spring Canyon, on north-facing slope, at edge of watercourse on moist drainages, *W. Niles s.n.*, 22 March 1996 (UNLV). These two localities constitute the second and third reports from the northern Mojave Desert, with the first from Washington County, Utah (Flowers 1973). *Syntrichia princeps* is distinguished from the related *S. ruralis* (Hedw.) Web. & Mohr by its (often) synoicous condition, and is disjunct from the western coast of North America to the Spring Mountains and Virgin Mountains of southern Nevada and southern Utah, respectively. *Syntrichia princeps* is one of several species in Utah known only from Washington County (Flowers 1973).

*Syntrichia ruralis* (Hedw.) Web. & Mohr

Nevada, Muddy Mountains, Valley of Fire State Park, 0.5 km south of "Mouse's Tank," sandstone bluffs on west side of road, elevation 700 m, *Stark & Bonine 3077, 3078* (UNLV). Oddly, *S. ruralis* is known from only two sites from the northern Mojave Desert, from Mohave County, Arizona (Haring 1961), and from the River Mountains in Nevada (Stark et al. 1998). The locality given represents one of the few sites known to the authors in the Mojave Desert where male, female, and sporophytic plants co-occur.

*Tortula atrovirens* (Sm.) Lindb.

Nevada, Clark County, Bitter Spring Valley, Echo Wash, gypsum formation ca. 1.6 km east of Bitter Spring, elev. 530 m, *Stark NV-2087* (UNLV); northern River Mountains, Lake Mead National Recreation Area, 5.6 km due east of Saddle Island, elev. 610 m, *Stark NV-139a* (UNLV); Newberry Mountains, Lake Mead National Recreation Area, Grapevine Canyon, 3.2 km north on Christmas Tree Pass Rd from Hwy 77E, beyond petroglyphs to the east, elev. 854 m, *Stark NV-39a* (UNLV). Only a single prior report exists from the northern Mojave Desert exists, and this as an incidental (Stark et al. 1998), thus indicating that the species is probably much more common than reports indicate. *Tortula atrovirens* was previously known as *Desmatodon convolutus* (Brid.) Grout.

*Weissia condensata* (Voit) Lindb.

Nevada, Clark County, foothills on northwest side of River Mountains, ca. 6.4 km from down-

town Henderson, elev. 671 m, *Stark NV-120* (UNLV, BUF). First report from southern Nevada and probably a state record. Reported from Arizona, southern Utah, Texas, and Mexico, *W. condensata* is a widespread species that also occurs in South America, Africa, and Europe (Flowers 1973, as *W. tortilis* (Schwaegr.) C. Muell.; Zander 1994c).

HEPATICOPHYTA

*Asterella californica* (Hampe) Underw.

Nevada, Clark County, Lake Mead National Recreation Area, Indian Hills, north of Devil's Cove, Gold Butte area, T20S, R70E, at base of limestone boulders, elevation 650 m, *W. E. Niles s.n.*, 6 March 1998 (UNLV); Spring Mountains, Red Rock National Conservation Area, near mouth of Red Rock Canyon near confluence with Red Rock Wash, T20S, R58E, S32, damp shaded soil beneath overhang at base of north-facing cliff, elev. 1450 m., *A. T. Whittemore 6887* (MO). Nevada state record. Known from Mohave Co., Arizona (Evans 1917) and from Riverside Co., CA, near Palm Springs (*S. B. Parish 3890*, CAS).

*Reboulia hemispherica* (L.) Raddi

Nevada, Clark County, Spring Mountains, Red Rock National Conservation Area, near Willow Springs, T21S, R58E, S5, shaded gorge, in cracks in cliff, elev. 1500 m, *A. T. Whittemore 6891* (MO). Nevada state record. This is the first report of this rather wide-ranging species from the Mojave Desert. *Reboulia hemispherica* is fairly common in New Mexico and eastern Arizona, but it is rare and local west of these states, currently known only from two collections from the northern Sierra Nevada in California and a few scattered sites in the Pacific northwest.

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# NOTEWORTHY COLLECTIONS

## CALIFORNIA

*BACCHARIS MALIBUENSIS* R. M. Beauch. & Henr. (ASTERACEAE).—Orange Co., [Santa Ana Mountains] North Ranch Policy Plan Area [proposed for inclusion in the NCCP], Fremont Canyon, N. of Santiago Creek and immediately S. of major stream fork [of the Fremont Canyon drainage], 33.7907°N 117.6801°W, UTM Zone 11 N3740484 E435012, ca. 305 m, 23 Aug 2000, Riefner & Wolf 20-732 (RSA).

*Previous knowledge.* *Baccharis malibuensis* was described by Beauchamp and Henrickson in 1996 (Aliso 14: 197–203) as a narrow endemic restricted to the Malibu Creek drainage in the Santa Monica Mountains, extreme western Los Angeles County. At that time, the species was known from 5 localities on private land within an area just over 18 km<sup>2</sup>, growing on volcanic and sedimentary substrates in chaparral, openings in scrub, and in the understory of *Quercus agrifolia* Née (Beauchamp & Henrickson 1996, *loc. cit.*).

*Significance.* The Riefner & Wolf collection of *B. malibuensis* from the Santa Ana Mountains represents the first record for that range, the first record for Orange County, and a disjunction of 93 km south from the southernmost station in the Santa Monica Mountains. At the Fremont Canyon site, the plant was rare, growing at the base of a north-facing slope in the understory of a *Q. agrifolia* riparian woodland along an intermittent stream course. Associated species reported for the site include *Symphoricarpos mollis* Nutt., *Heteromeles arbutifolia* (Lindley) Roem., *Rhamnus* sp., *Toxicodendron diversilobum* (Torrey & A. Gray) E. Greene, *Artemisia douglasiana* Besser, *Piptatherum milaceum* (L.) Cosson, and *Ambrosia psilostachya* DC. This region of Fremont Canyon is primarily underlain by marine sandstones of the Williams Formation, which consists of very resistant, cliff-forming, white to brownish-gray feldspathic sandstone, pebbly sandstone, and conglomeratic sandstone (Morton 1999, Open-File Report 99-172, U.S. Geological Survey).

Aside from the Palos Verdes headlands, the Santa Ana Mountains are the closest near-coastal range south of the Santa Monica Mountains. Two other taxa, *Dudleya cymosa* (Lem.) Britton & Rose ssp. *ovatifolia* (Britton) Moran and *Nolina cismontana* Dice, exhibit a similar pattern of disjunction between the Santa Monica and Santa Ana Mountains. It is not completely surprising, therefore, to find that *B. malibuensis* is present in both ranges. In the Santa Monica Mountains, *B. malibuensis* is known only from private lands and the documented occurrences are represented by populations of very small size, quite vulnerable to extirpation by development (Beauchamp & Henrickson 1996, *loc. cit.*). For this reason the species was added to list 1B of the California Native Plant Society's inventory of rare and endangered vascular plants, with rarity-endangerment-distribution (RED) of 3-3-3, their highest threat rating ([www.cnps.org/rareplants/inventory/6thEdition.htm](http://www.cnps.org/rareplants/inventory/6thEdition.htm)). At the present time it appears that *B. malibuensis* is also quite rare in the Santa Ana Mountains; only a single, pistillate, multi-branched subshrub approximately 8 dm high and 15 dm wide was located in 2000. Owing to the extremely rugged topography and relatively undisturbed character of the vegetation of this region it is likely that additional plants could be discovered in other

nearby canyons that were not explored in 2000. Since *B. malibuensis* is also known from west- and south-facing slopes in clearings and dense chaparral in the Santa Monica Mountains (Beauchamp & Henrickson 1996, *loc. cit.*) further surveys for *B. malibuensis* in similar habitats of the northern Santa Ana Mountains are warranted.

—STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

## COLORADO AND NEW MEXICO

*ERIGERON OCHROLEUCUS* Nutt. var. *SCRIBNERI* (Canby ex Rydb.) Cronquist (ASTERACEAE).—COLORADO: Weld County, rocky ridge 5.6 km N of Rockport, elev. 1830 m, T11N R66W sect. 6 E½ NE¼, 16 May 2000, Dorn 8222 (COLO, RM).

*Previous knowledge.* A range extension of 68 km from Albany County, Wyoming.

*Significance.* First report for Colorado.

*SALIX ARIZONICA* Dorn (SALICACEAE).—COLORADO: Conejos County, wet meadow along streamlet off Red Lake Trail Road 0.8 km from Hy. 17, elev. 3140 m, 37°04.7'N, 106°24.1'W, 6 July 2001, Dorn 8852 (COLO, MO, RM).

*Previous knowledge.* A range extension of 105 km from Rio Arriba and Taos counties, New Mexico.

*Significance.* First report for Colorado.

*SALIX DISCOLOR* Muhl. (SALICACEAE).—COLORADO: Larimer County, bank of South Branch Boxelder Creek at County Road 37, elev. 2195 m, 40°57.7'N, 105°14.8'W, 29 May 2001, Dorn 8752, same plant 10 July 2001, Dorn 8894 (COLO, MO, RM).

*Previous knowledge.* A range extension of 50 km from Laramie County, Wyoming.

*Significance.* First report for Colorado.

*SALIX WOLFII* Bebb var. *WOLFII* (SALICACEAE).—NEW MEXICO: Rio Arriba County, meadow along Osier Creek ca. 1.2 km SW of confluence with Rio de los Piños, elev. 2925 m, 36°59.6'N, 106°20.6'W, 5 July 2001, Dorn 8847 (MO, NMC, RM, UNM).

*Previous knowledge.* A range extension of ca. 40 m from adjacent Conejos County, Colorado or 2 km from nearest collection site in same county.

*Significance.* First report for New Mexico.

—ROBERT D. DORN, Box 1471, Cheyenne, WY 82003.

## IDAHO

*CRYPTOGRAMMA STELLERI* (S.G. Gmelin) Prantl (PTERIDACEAE).—Boundary Co., Upper Priest Falls on Priest River, 1 km south of British Columbia border, 48°59'N, 116°55'W, rare on seepy, crumbly calcareous rock around waterfall in forest of *Tsuga heterophylla* and *Thuja plicata*, with *Asplenium viride*, ca. 950–1050 m, 20 Jul 2001, T. Spribille 11177 (ID).



**Previous knowledge.** A widespread North American-Asiatic fern known from widely scattered localities in the western United States (E.R. Alverson, 1993, *Cryptogramma*. In: Flora of North America 2: 137–139) and infrequent in adjacent British Columbia (G.W. Douglas et al., 1991, Vascular Plants of British Columbia).

**Significance.** First report for Idaho, a range extension of approximately 330 km west from the nearest known locality on the east side of Glacier National Park, Glacier Co., Montana.

**VIOLA SELKIRKII** Pursh ex Goldie (VIOLACEAE)—Bonner Co., upper end of Priest Lake, along Ruby Creek, ca. 48°50'N, 116°55'W; frequent in riparian *Thuja plicata* forest, with *Tiarella trifoliata*, *Viola glabella* and *Oplopanax horridus*, ca. 730 m elev., 20 Jul 2001, T. Spribille & R. Merkel 11123 (ID).

**Previous knowledge.** A widespread circumboreal species, rare in western North America, where it is known from widely scattered localities in Alaska, British Columbia, Alberta, Colorado (E. Hultén, 1968, Flora of Alaska and Neighboring Territories), New Mexico (W.C. Martin & C.R. Hutchins, 1980, Flora of New Mexico) and Montana (T. Spribille et al., 2002, Noteworthy Collections, Madroño 49:55–58).

**Significance.** First report for Idaho, a range extension of approximately 150 km west from the nearest known locality in the Whitefish Range, Lincoln Co., Montana.

—TOBY SPRIBILLE, Kootenai National Forest, Fortine Ranger District, P.O. Box 116, Fortine, MT 59918 (current address: Herbarium, Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany; e-mail toby.spribille@gmx.de).

#### MONTANA

**ALNUS RUBRA** Bong. (BETULACEAE)—Lincoln Co., western Cabinet Mountains, Callahan Creek drainage, along Callahan Creek and North Callahan Creek at Montana/Idaho state line and up to 3 km east into Montana, 48°26'30"N 115°57'–116°00'W, in alluvial bottoms and on moist slopes with *Thuja plicata*, *Tsuga heterophylla* and *Betula papyrifera*, 850–915 m, 16 Jun 1998, T. Spribille & M. Arvidson 7788 (USFS Fortine District Herbarium, COLO, MONTU, MRC).

**Previous knowledge.** This primarily coastal species has a limited distribution in the interior and is usually associated with inland rainforest communities (Johnson & Steele, 1978, Northwest Sci. 52(3): 205–211; C.C. Lorain, 1988, Floristic history and distribution of coastal disjunct plants of the northern Rocky Mountains, M.Sc. thesis, Univ. Idaho). It is widespread along the Pacific Coast and is known from disjunct inland populations in British Columbia, Washington and Idaho.

**Significance.** First report for Montana, representing the eastern limits of species distribution, a contiguous range extension across the state line from nearby Boundary Co., Idaho. As in the Idaho locations, there appears to be introgression with *Alnus incana* ssp. *tenuifolia* in at least some individuals. The first reports of red alder from this area came from forest stand examination contractors who reported *Alnus* in the area as large as 59 cm dbh.

**AZOLLA MEXICANA** Presl. (AZOLLACEAE)—Ravalli Co., McCalla Creek, app. 2 km west of Stevensville,

46°30'20"N 114°07'40"W, locally common and forming small mats, with *Callitriche heterophylla* and *Elodea canadensis*, 1030 m, 18 Sep 1999, W.E. Albert 3261 (MRC). Verified by P.F. Stickney (MRC).

**Previous knowledge.** Widespread across the western states and British Columbia to South America, scattered east to the Mississippi River (T. A. Lumpkin, 1993, Azollaceae. In: Flora of North America 2: 338–342).

**Significance.** First report for Montana, probably introduced with recent disturbance, persisting and spreading in similar nearby drainages and a nearby slough. The nearest known collection stations are 320 km southwest and southeast, respectively, in Ada and Bannock Cos., Idaho (specimens at ID).

**BOTRYCHIUM PEDUNCULOSUM** W.H. Wagner (OPHIOGLOSSACEAE)—Lincoln Co., Big Creek, 48°44'30"N 115°28'30"W, rare in moonwort genus communities on floodplains under *Thuja plicata*, 975 m, 24 Jul 1996, J. Vanderhorst 5609 (MONTU); Big Creek, 48°46'N 115°27'W, 9 Aug 1997, J. Vanderhorst 5617 (MONTU); Cedar Creek, 10 km west of Libby, 48°24'35"N 115°40'59"W, with *Thuja plicata*, 1070 m, 1 Aug 1997, R. Ferriell s.n. (USFS Kootenai NF Herbarium); Quartz Creek, 17 km northwest of Libby, 48°30'50"N 115°42'07"W, with *Tsuga heterophylla*, *Thuja plicata* and *Athyrium felix-femina*, 910 m, 15 Aug 1997, R. Ferriell s.n. (USFS Kootenai NF Herbarium); Davis Creek, 20 km southwest of Trego, 48°31'37"N 114°57'40"W, in roadbed and powerline corridor, 1150 m, 22 Jul 1998, R. Ferriell RF98017 (USFS Kootenai NF Herbarium); Sanders Co., 0.8 km northeast of Noxon Rapids Dam, 47°57'53"N 115°43'21"W, mesic meadow, 735 m, 27 Jun 1999, R. Ferriell RF99014 (USFS Kootenai NF Herbarium). Vanderhorst 5609, 5617 determined by W. H. Wagner (MICH).

**Previous knowledge.** A rare species of northwestern North America from southwestern Saskatchewan west to British Columbia and Oregon, east of the Coast/Cascade Ranges (W.H. Wagner & F.S. Wagner, 1993, Ophioglossaceae. In: Flora of North America 2: 85–106).

**Significance.** First reports for Montana, a range extension of approximately 130 km east from Pend Oreille Co., Washington.

**CAREX CHALCIOLEPIS** Holm (CYPERACEAE)—Ravalli Co., Anaconda-Pintler Wilderness area, wet meadow that parallels both sides of the creek draining Hidden Lake, 45°55'10"N 113°33'00"W, 2500 m, Mooers & Mooers 998 (MONT). Determined by T. Spribille, verified by D.F. Murray (ALA).

**Previous knowledge.** A species of subalpine to alpine meadows in the southern and central Rocky Mountains, described by Holm (1903, Amer. J. Sci. 16: 17–44). Murray (1969, Brittonia 21: 55–76) expressed doubt as to the occurrence of this species in Montana, because the material available to him was too immature to be certain of its identity.

**Significance.** First report for Montana, representing the northern limits of species distribution, a range extension of over 300 km northwest from the nearest reported location in Park County, Wyoming.

**CAREX DEFLEXA** Hornem. var. *BOOTHII* L.H. Bailey (CYPERACEAE)—Beaverhead Co., Beaverhead National Forest, Stine Mtn., West Pioneer Range, growing in *Larix lyallii* grove, 2640 m, 21 Jul 1968, S.F. Arno 29 (MONTU); Beaverhead Co., Lima Peaks, one mile east of Garfield Mtn., 8 miles south of Lima, common forming small patches of turf in stony, quartzite-derived soil of an alpine

fellfield, 3030 m, 27 Jul 1989, *P. Lesica & S. Cooper* 4966 (MONTU); Missoula Co., Flathead National Forest, Lindy Peak, Mission Range, beneath stunted *Larix lyallii*, 2515 m, 1 Sep 1968, *S.F. Arno* 285 (MONTU); Missoula Co., Bitterroot Mtns., fellfield on Onehorse Ridge, Lolo Peak massif, 2575 m, 21 Jul 1971, *K. Lackschewitz* 2953 (MONTU); Ravalli Co., East Boulder Peak, growing in talus enclosure within alpine larch [stand], SE slope, 2710 m, 7 Aug 1968, *K. Lackschewitz & T. Fageraas* 596 (MONTU); Ravalli Co., dry, rocky crags, W-slope of the Castle Crags, 2590 m, 18 Aug 1970, *K. Lackschewitz & Stuart* 2365 (MONTU); Ravalli Co., NE slope of Canyon Peak, Canyon Lakes Basin, beneath alpine larch, 2590 m, 22 Aug 1971, *K. Lackschewitz* 3337 (MONTU); Ravalli Co., St. Joseph Peak, wind-timber zone, 2740 m, 24 Jul 1971, *K. Lackschewitz & Gouaux* 2979 (MONTU). All specimens determined by T. Spribille and verified by A.A. Reznicek (MICH).

**Previous knowledge.** Although previously reported for Montana by Rydberg (1900, *Flora of the Rocky Mountains*) and F.J. Hermann (1970, *Manual of the Carices of the Rocky Mountains and Colorado Basin*, USDA Agr. Handb. 374) as *Carex brevipes* W. Boott, this species was subsumed under *Carex rossii* Boott in Hook. by C.L. Hitchcock et al. (1969, *Vascular plants of the Pacific Northwest*, Vol. 1), and has since escaped mention in the floras of Montana. The species is distinct from *C. rossii* both morphologically and ecologically, being a distinctly subalpine to alpine taxon with an apparent affinity for *Larix lyallii* stands near the alpine timberline, in contrast to the more montane, xerothermic *C. rossii*. Furthermore, *C. deflexa* is more widespread across boreal North America than the primarily western *C. rossii*.

**Significance.** These reports reaffirm the presence of this species in Montana.

**CAREX LACUSTRIS** Willd. (CYPERACEAE)—Lake Co., small glacial pothole marsh ca. 6 km south of Swan Lake, 47°52'15"N 113°49'50"W, with *Carex utriculata* and *C. lasiocarpa*, 945 m, 15 Jul 1989, *P. Lesica* 4893 (MICH, MONTU); Swan River Valley, Lost Creek Fen, ca. 5 km south of village of Swan Lake, 47°52'55"N 113°49'42"W, in mossy saturated peat of fen, with *Betula glandulosa* and *Carex lasiocarpa*, 965 m, 19 Jun 1992, *J.S. Shelly & S. Chadde* 1652 (MICH). Both specimens determined by A.A. Reznicek (MICH).

**Previous knowledge.** A species of the Great Lakes and Great Plains, rarely as far west as Idaho (M.L. Fernald, 1942, *Rhodora* 44: 281–331; Great Plains Flora Committee, 1977, *Atlas of the Flora of the Great Plains*), north-central Alberta (J.G. Packer, 1983, *Flora of Alberta*), and reportedly also British Columbia, although this report was based on a misidentification (A. Ceska personal communication).

**Significance.** First reports of this species for Montana. It joins a suite of species of the eastern deciduous woodland region (e.g., *Carex comosa*, *Carex pallescens*, *Dryopteris cristata*, *Primula mistassinica*) represented by disjunct localities in northwestern Montana, northern Idaho and southeastern British Columbia.

**CAREX PALLESCENS** L. (CYPERACEAE)—Ravalli Co., Bitterroot Valley along Bass Creek, 46°34'35"N 114°09'11"W, uncommon in moist meadow bordering *Pinus ponderosa* and *Pseudotsuga menziesii* with *Juncus balticus*, 1020 m, 6 Jul 1997, *W. E. Albert* 3167 (MICH); Bitterroot Valley, app. 18.4 km south and 2.4 km west of Florence, 46°28'40"N 114°09'11"W, uncommon in seasonally-saturated meadow along a small stream with *Populus trichocarpa*, *Pinus ponderosa*, *Carex illota* and *C. lanu-*

*ginosa*, 1085 m, 11 Jun 2000, *W. E. Albert & B. Heidel* s.n. (MONTU); Bitterroot Valley, south of Hamilton at Cory Place, 46°12'05"N 114°10'05"W, along waterway, 1090 m, 27 Jun 1979, *J. Cory* 1917 (MONTU). *Albert* 3167 determined by B. Heidel, verified by A.A. Reznicek (MICH); *Cory* 1917 determined as *Carex torreyi* by K. Lackschewitz, annotated to *C. pallescens* by A.A. Reznicek (MICH).

**Previous knowledge.** An eastern species, introduced on Hornby Island, British Columbia from Europe or eastern North America (G.W. Douglas et al. 1994, *Vascular Plants of British Columbia*, Part 4), and recently discovered in Stevens Co., Washington, until recently not otherwise known from west of Great Lakes region.

**Significance.** First reports for Montana, a range extension of approximately 335 km southeast of Stevens Co., Washington (*Bjork* 3463, WS, ID). It is otherwise disjunct approximately 1700 km west from Duluth, Minnesota.

**CAREX PRAIREA** Dewey (CYPERACEAE)—Flathead Co., northern Salish Mountains, confluence of Lime and Magnesia Creek drainages, approximately 6.4 km south of Trego, 48°38'30"N 114°52'30"W, locally common in matted clumps over 8–10 acres of bog birch fen complex with *Potentilla fruticosa* and *Carex capillaris*, 1060 m, 25 Jul 1995, *F.J. Triepke* 24 (USFS Fortine District Herbarium); Flathead Co., northern Salish Mountains, Magnesia Creek drainage, Magnesia Fen, 48°37'30"N 114°52'30"W, very common and abundant in fen, with *Betula glandulosa*, *Carex leptalea* and *Tomentypnum nitens*, 1145 m, 21 Jun 1995, *T. Spribille* 3355 (MICH), *T. Spribille* 3358 (USFS Fortine District Herbarium); same location, 1 Aug 1995, *T. Spribille* 3902 (COLO); Flathead Co., northern Salish Mountains, Blessed Creek ca. 0.75 km above confluence with Sunday Creek, 48°49'40"N 114°32'20"W, in rich calcareous fen, local in small patches, 1325 m, *T. Spribille* 7749 (COLO). *T. Spribille* 3355 verified by A.A. Reznicek (MICH).

**Previous knowledge.** A widespread species of the boreal forest, *Carex prairea* has been reported from the western cordillera in Idaho (R. Davis, 1952, *Flora of Idaho*) and Wyoming (E. Hultén & M. Fries, 1986, *Atlas of North European Vascular Plants North of the Tropic of Cancer*, 3 vol.), although we have been unable to locate vouchers for these reports. In western Canada it is known from several sites in the Cariboo-Chilcotin region of central British Columbia (A. Roberts, 1983, *A Field Guide to the Sedges of the Cariboo Forest Region*, British Columbia B.C. Min. For., Land Management Rep. No. 14; T.M.C. Taylor, 1980, *The sedge family [Cyperaceae] of British Columbia*, Royal B.C. Museum Handb. #43) and from central Alberta (J.G. Packer, 1983, *Flora of Alberta*).

**Significance.** First reports for Montana, a range extension of ca. 420 km south from the nearest known stations in west-central Alberta.

**CAREX VAGINATA** Tausch (CYPERACEAE)—Lincoln Co., northern Salish Mountains, White Creek, just south of Forest Service Road 3529, 48°34'00"N, 114°56'30"W, 1200 m, in midmontane *Picea glauca* swamp with *Rubus pubescens*, and *Carex disperma*, 5 Jun 1996, *T. Spribille & F.J. Triepke* 5054 (USFS Fortine District Herbarium, MICH); Lincoln Co., northern Salish Mountains, fen on White Creek along FS Rd. 36, 48°33'45"N, 114°57'00"W, 1125 m, 17 Jul 1998, *T. Spribille & R.S. Wirt* 7938 (MONTU). *Spribille & Triepke* 5054 verified by A.A. Reznicek (MICH).

**Previous knowledge.** A widespread pan-continental species of the boreal forest from Alaska to Labrador (A.E.

Porsild & W.J. Cody, 1980, Vascular Plants of Continental Northwest Territories, Canada, Natural Museum of Natural Sciences, Ottawa), south to New York, Michigan and Minnesota.

**Significance.** First reports for Montana and the western contiguous United States, a range extension of about 120 km south from the nearest location mapped by T.M.C. Taylor (The sedge family [Cyperaceae] of British Columbia, Royal B.C. Museum Handb. #43, 1980) in the southern Rocky Mountain Trench of British Columbia.

**CENTAURIUM ERYTHRAEA** Rafin. (GENTIANACEAE)—Sanders Co., Cabinet Gorge Reservoir, road between Noxon and Heron on south side of reservoir, ca. 5 km south of mouth of Elk Creek, locally common where powerline maintenance road clearing connects to the main road. 48°02'N 115°52'30"W, 670–730 m, 25 Aug 1997, T. Sprill 7429 (COLO). Verified by W.A. Weber (COLO).

**Previous knowledge.** A Eurasian meadow species with medicinal uses, reported as established in northwestern North America from southern British Columbia (G.W. Douglas et al., 1990, Vascular plants of British Columbia, Part 2) south to California and inland to Idaho (C.L. Hitchcock et al. 1959, Vascular plants of the Pacific Northwest, Vol. 4).

**Significance.** First report for Montana, representing the most inland station in western North America.

**ERIOGONUM VISHERI** A. Nels. (POLYGONACEAE)—Carter Co., Powderville Road badlands, on the divide between Dry Creek and Whitetail Creek, 45°46'18"N 104°55'42", occasional on outcrops and outwash flats of Hell Creek Formation shale with *Allium textile*, *Musineon divaricatum* and *Elymus lanceolatus*, 948 m, 6 Jun 1997, B. Heide 1540 (MONT); same location, 12 Jul 1997, J. Vanderhorst 5732 (MONT, MONTU).

**Previous knowledge.** A regional endemic of the Great Plains, previously known only from North and South Dakota (Great Plains Flora Committee, 1986, Flora of the Great Plains).

**Significance.** First report for Montana, a range extension of approximately 100 km southwest from Slope County, North Dakota and 150 km northwest from Harding Co., South Dakota.

**LESQUERELLA DOUGLASII** S. Wats. (BRASSICACEAE)—Lincoln Co., Lake Koocanusa, Rexford Bench, 48°54'N 115°10'30"W, just west of Rexford along path; occurring infrequently and in small populations on sand in *Pinus ponderosa*/Purshia tridentata community, 775 m, 14 May 1999, F.J. Triepke & A. Stachurska 233 (COLO), same location, fruiting material, 26 Jun 2000, F.J. Triepke 246 (USFS Fortine District Herbarium). Triepke 246 verified by R. Hartman (RM).

**Previous knowledge.** A Columbia Basin species of Washington, Oregon and British Columbia, known from a string of disjunct populations in the Rocky Mountain Trench of southeastern British Columbia. Rollins (1993, The Cruciferae of Continental North America) suggested it was to be expected in northwestern Montana.

**Significance.** First report for Montana, a range extension of ca. 40 km from the nearest known location along the Elk River near Grasmere, British Columbia (Sprill 1760, UBC).

**MIMULUS RINGENS** L. (SCROPHULARIACEAE)—Chouteau Co., south shore of Missouri River, approximately 8 km east of Virgelle, 48°02'08"N 110°09'06"W, seasonally flooded sandbar with *Populus deltoides* seedlings, *Eleocharis palustris* and *Helenium autumnale*, 767 m, 7 Jul

2000, B. Heide 1552 (MONTU). Verified by R. Meinke (OSC).

**Previous knowledge.** This primarily eastern species is known only from widely scattered western stations in Colorado (W.A. Weber & R.C. Wittman, 1992, Catalog of the Colorado Flora: A Biodiversity Baseline), Idaho (R. Davis, 1952, Flora of Idaho), California (J.C. Hickman, ed. 1993, The Jepson Manual of the Higher Plants of California) and Washington (specimen at WTU).

**Significance.** First report for Montana, a range extension of at least 745 km west from Rolette Co., North Dakota.

**RIBES LAXIFLORUM** Pursh (GROSSULARIACEAE)—Lincoln Co., West Cabinet Range, south end of Little Spar Lake, 29 km SSW of Troy, 48°12'38"N 116°01'06"W, tall shrub field, 1675 m, 8 Sep 1997, E. Pederson 500 (MRC); same location, 26 Aug 1998, M. Arvidson & L. Ferguson 1015 (MRC). Both specimens verified by P.F. Stickney (MRC).

**Previous knowledge.** A Pacific coastal species, known inland from scattered stations in the Rocky Mountains of British Columbia (G.W. Douglas et al., 1990, Vascular Plants of British Columbia, Part 2), southwestern Alberta (C.L. Hitchcock & A. Cronquist, 1973, Flora of the Pacific Northwest), Colorado and New Mexico (A. Cronquist et al. 1997, Intermountain flora, Vol. 3, Part A.).

**Significance.** First report for Montana, a range extension of 13 km east from the nearest known location, at Halverson Creek, Bonner Co., Idaho, 1 km from the Montana state line (Pederson 26, MRC).

**SENECIO CONGESTUS** (R. Br.) DC. (ASTERACEAE)—Roosevelt Co., rangeland, no coll. date, received 11 Jun 1992, location information unavailable, Roosevelt County Extension Service s.n. (MONT). Determined by J. H. Rumely (MONT).

**Previous knowledge.** A pan-continental boreal wetland species known from Newfoundland to Alaska and south from South Dakota and Iowa (Great Plains Flora Committee 1986, Flora of the Great Plains) to Michigan (E.G. Voss, 1972–1996, Michigan Flora).

**Significance.** First report for Montana, a range extension of at least 30 km west from Divide Co., North Dakota.

**VENTENATA DUBIA** (Leers) Coss. & Dur. (POACEAE)—Ravalli Co., Skalkaho Creek, 46°09'57"N 113°55'54"W, common on dry roadsides with *Poa compressa*, *Stipa comata*, 1219 m, Jul 1995, W. E. Albert 3131 (MONT). Verified by J. R. Rumely (MONT).

**Previous knowledge.** A southern European species of dry grasslands introduced in western and northeastern North America, known from Idaho and Washington (C. L. Hitchcock et al. 1969, Vascular Plants of the Pacific Northwest, Vol. 1), southwestern British Columbia (G. W. Douglas et al., 1994, Vascular Plants of British Columbia, Part 4) and Utah (L. Allen & M. Curto, 1996, Madroño 43:337–338).

**Significance.** First report for Montana, a range extension of approximately 120 km east from Idaho Co., Idaho.

**VIOLA SELKIRKII** Pursh ex Goldie (VIOLACEAE)—Lincoln Co., Whitefish Range, Grave Creek, on south bank of creek ca. 2 km downstream of Williams Creek confluence, 48°50'45"N 114°49'45", in alluvial mixed forest of *Betula papyrifera* and conifers, with *Aralia nudicaulis* and *Symphoricarpos albus*; infrequent, only 30–40 plants found; 1030 m, 8 Jun 1999, T. Sprill & A. Stachurska 9081 (BHO). Verified by H. Ballard Jr. (BHO).

*Previous knowledge.* This circumpolar boreal species is found in North America primarily in the eastern deciduous forests, but is also known only from widely scattered localities in the Rocky Mountains south to Colorado (cf. E. Hultén, 1968, Flora of Alaska and Neighboring Territories) and New Mexico (W.C. Martin & C.R. Hutchins, 1980, Flora of New Mexico).

*Significance.* First report for Montana, a range extension from southeastern British Columbia.

—TOBY SPRIBILLE, Kootenai National Forest, Fortine Ranger District, P.O. Box 116, Fortine, MT 59918 (current address: Herbarium, Department of Systematic Botany, Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, D-37073 Göttingen, Germany; e-mail toby.spribille@gmx.de); BONNIE HEIDEL, Montana Natural Heritage Program, 1515 E 6th Ave., Helena, MT 59620 (current address: Wyoming Natural Diversity Database, University of Wyoming, P.O. Box 3381, Laramie, WY 82071-3381, e-mail bheidel@uwoyo.edu); WALLACE E. ALBERT, 3653½ Silverthorn Drive, Stevensville, MT 59870; F JACK TRIEPKE, Kootenai National Forest, Fortine Ranger District, P.O. Box 116, Fortine, MT 59918; JIM VANDERHORST, Natural Heritage Program, West Virginia Division of Natural Resources, P.O. Box 67, Ward Rd. Elkins, WV 26241-0067; and G. MICHAEL ARVIDSON, Kootenai National Forest, Three Rivers Ranger District, 1437 Hwy 2 N, Troy, MT 59935.

#### OREGON

*HIERACIUM CAESPITOSUM* Dumort. (ASTERACEAE).—Wallowa Co., along Bear Creek Road, ca. 2 km S of Wallowa, with *Dactylis glomerata*, *Phleum pratense*, and

*Pseudotsuga menziesii*. Also in pastures, along logging trails but absent in adjacent undisturbed forest, and along roads and riparian areas bordering Bear Creek, elev. 1090 m, T1S R42E sect. 3, Long. 117.55, Lat. 45.48, 23 July 2000, Brooks (OCS #197099); T1S R42E sect. 15, 17 July 2001, Dwire 1728 (OSC) (Verified by K. L. Chambers, OSC). Distribution extends south along the Bear Creek Trail into the Eagle Cap Wilderness, and north in the riparian areas bordering the Wallowa River.

*Previous knowledge.* This species is also known as *Hieracium pratense* Tausch, an outdated synonym appearing in Hitchcock and Cronquist (1973) and other western floras. Native to Eurasia, meadow hawkweed was probably introduced into the United States in the 1820's, and was first reported in the Pacific Northwest in Pend Orielle Co., Washington in 1969. It has become widespread throughout Washington, northern Idaho, and northwestern Montana (Wilson et al. Rangelands 19:18–23, 1997; Toney et al., Northwest Science 72:198–209, 1998). It is spreading rapidly, primarily in montane meadows, pastures, and disturbed areas along roads and hillsides. Meadow hawkweed is a tenacious invader, and is listed as a noxious weed in Washington (Class B), Idaho, and Montana (Category 2).

*Significance.* First report of the species for Oregon. Although present in the Bear Creek drainage, Wallowa Co. for perhaps 10 years, meadow hawkweed was only recently distinguished from native hawkweeds. An additional unvouchered population of *Hieracium caespitosum* has been reported from Hood River Co., Oregon.

—KATHLEEN A. DWIRE, Department of Forest Science, Oregon State University, Corvallis, OR 97331-5752, and CATHERINE G. PARKS, USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, La Grande, Oregon 97850.

## ERRATUM

In Volume 48, No. 2, there was a typographical error in the title of the paper by Dieter Wilken (pages 116–122). The correct title should be

A new *Ipomopsis* (Polemoniaceae) from the southwest USA and adjacent Mexico.



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# MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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CATALOGUE OF NON-NATIVE VASCULAR PLANTS OCCURRING  
SPONTANEOUSLY IN CALIFORNIA BEYOND THOSE ADDRESSED IN  
*THE JEPSON MANUAL*—PART I

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ABSTRACT

A catalogue of 315 non-native vascular plant taxa documented as occurring spontaneously in California beyond those addressed in *The Jepson Manual: Higher Plants of California* is presented. The catalogue was compiled from new collections by the authors and others, previously existing herbarium specimens, formal publications, other printed reports, and direct communications with field botanists. Only reports backed by herbarium vouchers are accepted as adequately documented. Of the 315 species, 58 are fully or sparingly naturalized in relatively undisturbed wildland habitats, 53 are naturalized in disturbed areas, 34 are tenuously established or locally persisting, 13 are non-escaped weeds of greenhouse or similarly cultivated environments, 43 are presumed to be non-persisting casuals (waifs), for 110 there is no current information or observations available, and 4 have likely been extirpated. In addition, 13 reported taxa are here specifically excluded as based on erroneous information. Taxa highlighted as already being fully naturalized or potential pests are *Amaranthus rudis*, *Brassica fruticulosa*, *Boehmeria cylindrica*, *Calystegia silvatica* subsp. *disjuncta*, *Cabomba caroliniana*, *Cotoneaster lacteus*, *Crataegus monogyna*, *Dittrichia graveolens*, *Fumaria capreolata*, *Geranium purpureum*, *Geranium rotundifolium*, *Hedera canariensis*, *Limnium laevigatum*, *Maytenus boaria*, *Pyracantha crenatoserrata*, *Salvinia molesta*, *Trifolium tomentosum*, and *Verbascum olympicum*.

Key Words: Weeds, non-native, invasive plants, pest plants, voucher specimens.

The significance of invasive non-native plants has recently gained prominence, as evidence mounts for both the environmental and economic devastation such invasions can cause. A recent issue of *BioScience* (51[2] Feb. 2001), for example, is devoted to the topic of “Global Movements of Invasive Plants and Fungi.” On the national level, various legislative initiatives have been proposed to address the problem, such as the Harmful Nonnative Weed Control Act (S. 198). At the local level, Weed Management Areas, established through the

coordinated efforts of public and private agencies and organizations, now blanket most of California.

Obviously, for all of these efforts to work properly, accurate and comprehensive information needs to exist on which non-native plants occur within the area of concern and what potential level of threat they represent. While the average citizen might assume that this information is readily available, especially in this age of electronic databases, the reality is unfortunately otherwise. This is primarily because, although a broad spectrum of professional biologists and amateur enthusiasts eagerly hunt down and keep track of rare native species, non-natives have been historically under-reported if not outright ignored. As a result, our existing knowledge of the identity, occurrence, frequency,

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and distribution of non-native plants is often sketchy or preliminary.

California is by no means an exception to this rule, and the incomplete coverage of non-native species was one of the acknowledged shortcomings of *The Jepson Manual: Higher Plants of California* (Hickman 1993), which otherwise represented the state-of-the-art coverage of California plants at the time of its publication. In a subsequent statistical analysis of the numbers and distribution of the non-native taxa reported in the *Manual* (Rejmanek and Randall 1994), mention was made of some clearly naturalized plants that were missing, but no compilation was attempted. As a precursor tally by Hrusa and Ertter, over 70 non-native plant taxa beyond those included in the *Manual* were noted as naturalized in California (Ertter 2000). Moreover, the composition, frequency and distribution of plants in a given area is not static; this is particularly a feature of the non-native component, but even for native plants frequent updates to floristic accounts are necessary to maintain currentness (Yatskievych and Raveill 2001). The following catalogue is presented as the first installment of a continuing comprehensive effort to follow through on this preliminary note by compiling existing reports and documenting new occurrences of plant taxa that occur spontaneously in California but which are not treated in *The Jepson Manual*. Such cataloguing is intended to serve several functions: To help field botanists and consultants identify unknown species they come across during survey activities; to assist in the recognition of introduction pathways; and finally to provide further raw material for study of the invasion process itself.

#### MATERIALS AND METHODS

*Data sources.* Records of non-native vascular plants reported as growing without cultivation in California were reviewed and compiled. Data sources consisted of herbarium specimens, formal publications, other printed reports, and verbal communications with field botanists. Primary were our own and others' plant collections; secondary were the numerous published local California floras and verbal reports provided to one or more of the authors. We have also included detailed records as available for most of those taxa mentioned by Rejmanek and Randall (1994) as absent from *The Jepson Manual*. Because of the inevitable potential for misidentification, and following standard taxonomic practice, only reports that were backed up by hard documentation in the form of voucher specimens deposited in a publicly accessible herbarium are included in the current catalogue; this includes both those observed by one of the authors, stated in publication that such a voucher does exist, or verified by herbarium staff that one does exist. For example, the following taxa listed in Rejmanek and Randall (1994) are not included in Part I of the

current catalog because testifying vouchers could not be located: *Cordyline australis* (Forst.f.) Endl. (Liliaceae s.l.), *Cutandia memphitica* (Spreng.) Richt (Poaceae) and *Dodonaea viscosa* Jacq. (Sapindaceae). Of these taxa, a *Cordyline* has been observed by Hrusa at Salt Point, Sonoma Co., but a voucher confirming the specific application has not yet been acquired. The other two also may be established in California, but neither have as yet been so verified by the deposition of annotated specimens.

Many of the printed or verbal reports were from federal and state agency botanists, native plant society members, weed control groups, and other unpublished sources. Of particular importance were the plant samples submitted for identification by land managers, owners, farmers, ranchers, et al. to one or more herbaria. From these sources exact collection locality and ecological situation were sometimes difficult to ascertain, and the material provided was sometimes too poorly preserved to allow for more than an equivocal determination. The result was that, until field confirmation or better collections can be obtained, some reports currently remain unverified and are thus excluded from this compilation. Nevertheless, the value of the cooperation of landowners, land managers, or other field people cannot be overstated.

At the same time, the resultant catalogue is more than a simple report compilation. All reports were subject to verification by one or more authors, who also had the responsibility of determining naturalization status. Correspondence with and the assistance of staff at herbaria worldwide were needed in the effort to track down documenting specimens for some taxa reported for California. Although one cannot absolutely prove the absence of a specimen, by a preponderance of evidence some putative records were excluded, including several in published sources. For those taxa where a specimen was available, extensive identification efforts were often required to confirm identity, involving both worldwide taxonomic literature and herbarium specimens. In some particularly difficult cases, voucher specimens were sent to the appropriate specialist for identification or verification. Other problems, both taxonomic and nomenclatural, were resolved by electronic correspondence with the appropriate specialist, including several in Eurasia. Taxa reported for California, but for which documenting vouchers appear to be absent, and others determined on examination to be misidentified or erroneously reported, are listed and discussed in the RESULTS section.

*Scope of inclusion.* Our decision of what to include in the catalogue was based on three criteria: 1) The plant occurs spontaneously in California. "Spontaneous" as used here encompasses not only fully naturalized populations but any evidence of successful reproduction or initial appearance inde-

pendent of targeted cultivation, including casuals, garden escapes, and weeds of greenhouse, nursery, garden, lawn, and agricultural field. This exceptionally broad definition was chosen to capture the possible first appearance of potentially invasive species. However, long-persisting individuals that were intentionally planted, such as trees near abandoned homesites are not included unless they show evidence of successful reproduction, either sexual or vegetative; 2) The species was not addressed in *The Jepson Manual*, not even as an equivocal mention subordinate to another taxon. For example, *Mentha spicata* L. var. *longifolia* L. (Lamiaceae) is not included in the catalogue because it is mentioned in the *Manual* under *M. spicata* var. *spicata*, even though the entry is somewhat ambiguous and the variety is now fully documented as being naturalized in California. Likewise, we do not report new regional occurrences for species already included in the *Manual* (e.g., plants reported only for northern California that are documented from the southern part of the state as well); 3) At least one reported locality is documented by a voucher specimen deposited in a publicly accessible herbarium. Among the authors, at least fifteen vouchers were specifically prepared for reports that had not previously been so documented. It should be recognized that a statement in print that a voucher was made does not guarantee that one was indeed deposited and it is possible that some taxa included in this catalogue will eventually, after further research, be found to be unverified. In addition, specimens proving occurrence, but held in private collections were not included until a specimen or duplicates were made available for public scrutiny.

**Catalogue format.** Individual taxon records in the catalogue are formatted as follows:

**TAXON NAME:** Scientific name and author in accordance with the most recently available references (e.g., International Plant Names Index [<http://www.ipni.org/>]; *Flora of North America North of Mexico*; Flora Europaea on-line [<http://www.rbge.org.uk/forms/fe.html>]; Catalogue of New World Grasses [<http://mobot.mobot.org/W3T/Search/nwgc.html>]). In cases of conflicting recent treatments, final decisions were based on our collective judgement.

**DISTRIBUTION (D):** Reported occurrences in geographic subdivisions of California as described in *The Jepson Manual*, arranged alphabetically.

**CURRENT STATUS (CS):** A brief description of current status as can best be determined. There is disagreement among invasion ecologists as to the scope of the term "naturalized" (Richardson et al. 2000). We follow the terminology of Richardson et al. but split their "naturalized" into subcategories: 1, "naturalized in wildlands", and 2, "naturalized (outside of wildlands)". It is recognized that differential occupation of these habitats is not mutually exclusive, that assignment to one or the other category may be subjective, and that it is in addition

a rare situation that, in California, has not been "disturbed" at some time in the past. We nevertheless find the additional information provided in a classification distinguishing "naturalized in wildlands" and "naturalized (outside of wildlands)" potentially useful. This is because we feel that weedy species with a propensity to invade relatively natural or undisturbed areas are of different concern and may exhibit different ecological or reproductive strategies than are those plants which, although perhaps well-established, are restricted to agricultural conditions, roadsides or other heavily disturbed sites. The category "NCI" (no current information) needs some explanation. In general these are plants confirmed to have occurred at one time in California, but for which no immediate information is available as to their continued presence, rate of spread, or naturalization. Many records placed here could be assigned to another category based on the label data, but we preferred to maintain a conservative position on records that were often more than thirty years old, that is, these plants may be gone, or have spread widely during the ensuing years and we would be amiss in implying more knowledge about their current status than we actually have.

Naturalization categories are described and standardized abbreviations, as used in the catalogue, are introduced and described in Table 1.

**DOCUMENTATION (DOC):** Reports are arranged alphabetically by county (in bold) as either a literature citation for previously published reports, or as specimen citation for newly documented occurrences. Duplicate specimens might be housed in additional herbaria beyond those cited. Herbarium abbreviations are as used in *Index Herbariorum* (<http://www.nybg.org/bsci/ih/ih.html>). Generally literature cited as documentation includes specimen citations; however, collection or accession numbers, collectors names, dates and other details of location and habitat are only occasionally available in these sources. We expect that published floristic compilations maintain professional standards, and for published records where the specimen location is not specifically cited, the institution with which the author is or was affiliated houses the majority of the documented material. Known misapplications or misidentifications based on cited literature sources alone should be brought to our attention.

**NOTES:** Additional discussion or explanation as required or available, such as nomenclatural problems, history of introduction or evidence of invasiveness. In addition, for taxa believed to be becoming common or rapidly expanding their ranges, a short comparison among similar species and/or identification clues are provided.

## RESULTS

A total of 315 non-native vascular plant species meeting the criteria for inclusion are listed in Ap-

TABLE 1. CURRENT STATUS CATEGORIES.

Catalogue abbrev.	Description
NW	Naturalized in wildlands: A population that appears to be successfully propagating (sexually or vegetatively) and maintaining itself in a wildland situation.
N	Naturalized (outside of wildlands): A non-wildland population that is apparently of sufficient size or distribution to make the chances of its disappearance due to stochastic fluctuation negligible.
TEN	Persistence tenuous: A wildland or non-wildland population that is of few enough individuals to make the chance of disappearance via stochastic fluctuation a possibility.
C	Casual: Synonymous with "waif" as used in <i>The Jepson Manual</i> to describe a spontaneous occurrence that shows no evidence of successful propagation and spread.
GH/C	Greenhouse, nursery, garden weed: Non-escaped weed of greenhouse, nursery, garden, or other highly cultivated environment.
NCI	No current information: Plants confirmed to have occurred at one time in California, but for which there is no immediate information available as to the continued presence, rate of spread, or naturalization. Many records placed here are assignable to another category based on the label data, but we prefer not to categorize these without more current information.
EXT	Extirpated: Or reported as such. Habitat alteration or eradication programs in place have either eliminated these taxa from California or have nearly done so.

pendix 1 and itemized in detail (Appendix 2). Both lists are organized as in *The Jepson Manual*, with Appendix 1 intended to facilitate the location of names in Appendix 2. The classification used in the catalogue to convey current naturalization status is summarized in Table 2. If a taxon had populations that were classifiable in different categories, the taxon as a whole was included in the category indicating more complete naturalization. For example, *Salvinia molesta* D.S. Mitch. (Salviniaceae) has several populations well-naturalized in both wildland (NW) and non-wildland sites (N), plus is known several relatively small, localized populations from private ponds (classed as TEN); it was thus classified as naturalized (NW) for the summary statistics.

A subset of included species have the potential to achieve or have already achieved significant naturalized distributions or are pest plants, either as rapidly spreading invasive species (e.g., *Dittrichia graveolens* (L.) Greuter, Asteraceae) or as first California appearances of well-known pest plants that were immediately targeted for eradication (e.g., *Salvinia molesta*). These were taxa rapidly expanding their former ranges, serious invaders in other

parts of the world, plants already widespread and relatively commonly encountered, or plants apparently widespread but not heretofore correctly identified [e.g., *Hedera helix* in part = *Hedera canariensis* Willd., (Araliaceae)]. The plants in this subset are listed in Table 3. They are provided a longer discussion and identification clues within their individual Catalogue entries.

*Excluded taxa.* It is important to note also the number of putative reports that were excluded from the current catalogue not from lack of documentation, but because the reports were determined by the authors to be based on erroneous information. The importance of accurate identification of non-native naturalizing taxa cannot be overstated, there are numerous examples to show how control was only achieved once the proper identity of a pest was determined. A notable example is *Salvinia molesta* (Thomas and Room 1986); a similar, but currently unresolved example from California involves the genus *Salsola* (Chenopodiaceae) (M. Pitcairn personal communication). Due to the taxonomic and nomenclatural complexities of name application to non-native taxa, the following list of thirteen (13) excluded reports is certainly not exhaustive:

*Achnatherum clandestinum* (Hack.) Barkw. (Poaceae): Misapplied in California to the similar *A. brachychaetum* (Godr.) Barkw. Plants from Monterey Co. sometimes identified as *A. clandestinum* have been recently redetermined by Barkworth (UTC) as *A. brachychaetum*. The identity of a specimen reported as this (Barkworth 1993), from San Luis Obispo Co., remains unverified, but a possible duplicate (or second collection from the same site by the same collector) at UC was annotated by Barkworth as *A. caudatum* (Trin.) Jacobs, a taxon highly similar to and perhaps conspecific with *A. brachychaetum* (see Vickery et al. 1986) suggesting

TABLE 2. CURRENT STATUS SUMMARY. Explanation and definition of individual categories are provided in Table 1.

Definition	Catalogue abbrev.	Total
Naturalized in wildlands	NW	58
Naturalized (outside of wildlands)	N	53
Tenuous/locally persisting	TEN	34
Greenhouse, nursery, garden weed	GH/C	13
Casual	C	43
No current information	NCI	110
Extirpated	EXT	4

TABLE 3. POTENTIALLY SIGNIFICANT PLANTS. Fully naturalized species or first California appearances of well-known pest plants.

Taxon	Summary of current plant behavior and status
<i>Amaranthus rudis</i>	Well-established in widely separated localities.
<i>Brassica fruticulosa</i>	Rapidly spreading in mostly disturbed areas.
<i>Boehmeria cylindrica</i>	Becoming common in the upper Sacramento River delta.
<i>Calystegia silvatica</i> subsp. <i>disjuncta</i>	Widespread in coastal areas, previously misidentified.
<i>Cabomba caroliniana</i>	Rapidly expanding, well-established aquatic invader. Dominant in some Sacramento River delta locations.
<i>Cotoneaster lacteus</i>	Becoming locally common, expected more widely.
<i>Crataegus monogyna</i>	Appearing in widely separated regions, often in stable habitats.
<i>Dittrichia graveolens</i>	Rapidly expanding.
<i>Fumaria capreolata</i>	Unrecognized, probably more common than previously thought, likely expanding.
<i>Geranium purpureum</i>	Rapidly becoming more abundant.
<i>Geranium rotundifolium</i>	Widespread; overlooked previously, or rapidly expanding.
<i>Hedera canariensis</i>	Persistent invader of forest and woodland understories; previously confused with or included in <i>H. helix</i> .
<i>Limnobium laevigatum</i>	Rapid colonizer of open, still water, at low elevations. Can dominate to the exclusion of all other aquatic species.
<i>Maytenus boaria</i>	Aggressive invader of burns, forming long-lasting seedbanks.
<i>Pyracantha crenatoserrata</i>	Widespread; invader of mesic ditchbanks, roadside depressions, open shorelines.
<i>Salvinia molesta</i>	Recent aquatic introduction into California where spreading in the Colorado River and canal system.
<i>Trifolium tomentosum</i>	Widespread; previously overlooked or misidentified.
<i>Verbascum olympicum</i>	Naturalized in wildland habitat, expanding for more than 20 years.

that it may also be that taxon. Relationships among *A. clandestinum*, *A. caudatum* and *A. brachychaetum* need critical review.

*Dichondra repens* Forst. & Forst.f. (Convolvulaceae): Misapplied in California. Acc. to Hortus III (1976) material cultivated as *D. repens* is actually *D. micrantha*. See comments in the catalogue under the latter taxon.

*Glyceria declinata* Bréb. (Poaceae): Acc. to Leppig, all specimens of putative *Glyceria declinata* from California are indistinguishable from *G. occidentalis*. A discussion and treatment of variation in California *Glyceria occidentalis* is currently in preparation by Leppig. See also comments by Soza, Provance and Sanders (2000).

*Humulus americanus* Nutt. *sensu lato* (Cannabaceae): The voucher for the report in Smith (1973, pg. 92), has not been located, but a new collection from the same locality (Echo Summit Lodge, El Dorado Co.) by Steve Matson has been verified by E. Small as *H. lupulus* var. *neomexicanus* A. Nelson & Cockerell. In Small's treatment of *Humulus* in Flora of North America North of Mexico (3: 384–387, 1997), *H. americanus* has been split among several varieties of *H. lupulus* native to North America: var. *lupuloides* E. Small, var. *neomexicanus*, and var. *pubescens* E. Small. Although Small's treatment reports var. *neomexicanus* from California, this apparent introduction is the only currently confirmed occurrence of the taxon in California. We are rejecting the presence of *H. americanus* s.l. because this name also applies to forms

of *H. lupulus* (vars. *pubescens* and *lupuloides*) not in California.

*Hydrocharis morsus-ranae* L. (Hydrocharitaceae): Reports have all been misidentifications of, or misapplications to, *Limnobium laevigatum*. Both of these taxa are often called “frogbit”, probably the source of the identity confusion. *H. morsus-ranae* is a possible threat to northern and high elevation lakes in California, but has not yet been confirmed in California outside of cultivation.

*Nothoscordum bivalve* (L.) Britton (Liliaceae *sensu lato*): Apparently misapplied to *Nothoscordum gracile* (Ait.) Stearn s.l. (including *N. borbonicum* Kuntze = *N. inodorum* in the Jepson Manual). The cited location in Beauchamp (1986), “garden weed in Fallbrook” has a corresponding specimen at CDA of *N. inodorum sensu auct.* (= *N. gracile* or *N. borbonicum*).

*Passiflora mollissima* (Kunth) L.H. Bailey (Passifloraceae): Acc. to determinations by D. Goldman (BH) this name has been misapplied to *P. tarminiiana* Coppens & Barney and *P. mixta* L.f., both of which are established in California. See d'Eckenbrugge et al. (2001).

*Polypogon elongatus* Kunth (Poaceae): Misapplied to *P. imberbis* (Phil.) Bjorkm. See catalogue for more information.

*Pueraria lobata* (Willd.) Ohwi (Fabaceae): Verbal reports of kudzu vine in California have all been traced to native plants of *Vitis californica*. *Pueraria* has been cultivated in California as a curiosity, but in general, does not thrive under our dry

TABLE 4. TIMING OF REPORTING FOR NEW CALIFORNIA RECORDS OF TAXA INCLUDED IN THE CURRENT CATALOGUE IN RELATION TO PUBLICATION OF THE JEPSON MANUAL.

No. of taxa	Relationship to <i>The Jepson Manual</i>
129	Discovered prior to the <i>Manual</i> but either not identified or a report not published.
110	Discovered (published report or not) subsequent to the <i>Manual</i> .
63	Discovered and a report published prior to the <i>Manual</i> .
11	Re-determination of pre- <i>Manual</i> species.
2	Accidentally excluded from the <i>Manual</i> , but the taxonomic treatment was completed and submitted prior to publication.

Mediterranean climate. Locations discovered in northern Oregon in 2000 do apparently flower and fruit and are currently under pest evaluation.

*Salvia pratensis* L. *sensu stricto* (Lamiaceae): Thomas C. Fuller collections from the region of Yreka (Siskiyou Co.) cited in Munz, P.A. (1968, pg. 103) as *S. pratensis* have been redetermined at KW as *Salvia virgata* Jacq. See entry in the catalogue under that species for details.

*Sieglingia decumbens* (L.) Bernh. (Poaceae): Misapplied in Matthews (1997) to *Tribolium obliterum* (Hemzl.) Renvoize, first reported for North America in this catalogue. Cited also in Hitchcock and Chase (1950) as “escaped from cultivation, Berkeley”, but no confirming evidence or specimens have been located.

*Spartina maritima* (M.A. Curtis) Fern. (Poaceae): Misapplied to *Spartina anglica* C.E. Hubb. For detailed explanation see Spicher and Josselyn (1985).

*Spartina spartinae* (Trin.) Merr. (Poaceae): Misapplied to *S. densiflora* Brongn. Reported from Humboldt Bay (Gerish 1979; Spicher and Josselyn 1985) and in Marin Co. at Greenwood Cove near Tiburon [Aug. 11, 1982, *M.P. Wells s.n.* (CAS, CDA)].

As a further complication, individual occurrence reports can be erroneous even if the plant itself is documented to occur spontaneously in California. As a particularly convoluted example, *Amaranthus rudis* (Amaranthaceae), which is included in the current catalogue on the basis of multiple documented reports, had previously been cited in print (Munz 1974) only on the basis of a specimen from Pala in San Diego County, as *A. tamariscinus* Nutt. (misapplied to *A. rudis*). As it turns out, a duplicate of the voucher specimen (*Townsend s.n.*, housed at CDA) has been re-determined as *A. palmeri* S. Wats. In other words, the report of *A. rudis* from near Pala in southern California is erroneous, even though other, mostly more recent reports substantiate the existence of this midwestern native in northern California. This example likewise underscores the critical need to have available and examine vouchers to confirm their identification.

DISCUSSION

*Relation to the Jepson Manual.* *The Jepson Manual: Higher Plants of California* (Hickman 1993)

has for the past nine years provided California botanists with a new “standard” reference, supplanting the more than thirty-year old *A California Flora* (and its 1968 *Supplement*) by P.A. Munz and D.D. Keck. As earlier noted, non-native plants have historically been under-collected. Because floristic works such as the *Manual* used herbarium collections as the fundamental scientific standard, the result has been a general under-representation of non-native species. It is hoped the current paper, along with the burgeoning interest in non-native taxa as potential pest plants, will reverse this tendency.

In addition to those species that were omitted from the *Manual* because of the lack of accessible herbarium documentation, others were not included for a variety of reasons. In particular, the Jepson Manual Project deliberately excluded ‘casual’ (‘waif’) species, unconfirmed naturalization reports, or material apparently persistent from cultivation. While this was a reasonable decision for the *Manual*, we believe that even these marginal occurrences are worth reporting, given that all taxa that are now naturalized and well-established components of the State flora began as rare casuals or as small populations. Finally, there are plants in the current catalogue that have appeared as spontaneous occurrences in California subsequent to the closure of treatments for the *Manual*.

Worth mentioning in particular are those naturalized taxa that were reported in *A California Flora* or adequately documented in the intervening period but which were not treated in the *Manual*. The reasons these taxa were excluded are diverse. Some had been included in *A California Flora* but current information as to their naturalization status was not available. For others, individual authors may have decided that the inclusion of marginally established or rarely encountered weeds unnecessarily complicated identification keys and/or in general did not benefit the majority of users. Again, while this rationale may have been justified for the purposes of the *Manual*, this excluded group of plants is included in the current catalogue in order to assist those who have diverse interests concerning invasive taxa.

The temporal relationship of species in the current catalogue to *The Jepson Manual* is summarized in Table 4.



*Significance of new reports.* The often pestiferous nature of the most prominent weeds in California is well-recognized by the layman and professional alike (e.g., Bossard et al. 2000). What is not so universally understood is that these widespread and/or noxious pests generally began their occupation of California as seemingly innocuous roadside waifs, occasional garden volunteers, minor seed source contaminants, or localized populations remaining for some time in other non-prominent situations. The California Dept. of Food and Agriculture (CDFA) rates noxious weeds, and applies control efforts accordingly, not by their current affect on agricultural economics, but by their potential effect, the position being that control is both most biologically and cost effective when the populations are small, before the plant has become a widespread, established pest. Data have been assembled and published in support of this position (Bayer 1999). Although CDFA is concerned primarily with weeds affecting agricultural endeavors, wildland pests are no different nor are these conditions mutually exclusive; it is important to aggressively control these organisms before they become too widespread for control to be effective or eradication possible. Addressing only the most widespread and well-established weeds in California leaves a gap in our knowledge that may affect the future of California's agricultural activities, pristine wildlands and outdoor recreation areas. That this is an important gap may be recognized when one considers that every presently widespread weed in California began long ago as a "casual" [*Centaurea solstitialis* L. (Asteraceae), *Lepidium latifolium* L. (Brassicaceae)], or "occasional garden escape" [*Cytisus scoparius* (L.) Link, *Genista monspessulana* (L.) L. Johnson (both Fabaceae)].

While it cannot be specifically claimed that any plant appearing in this catalogue will ultimately become more than even a local pest, the naturalization of non-native plants may ultimately have long-lasting impacts. The truth of this statement is dramatically evident when perusing S. B. Parish's 1920 synopsis of immigrant plants of southern California, in the number of species that were merely present as scattered waifs in 1920 but which are now both fully naturalized and widespread. For example, *Potamogeton crispus* L. (Potamogetonaceae) was known in California from a single collection at Corona in 1918, while *Pennisetum villosum* R. Br. (Poaceae) was a "local fugitive from cultivation" that Parish was aware of only from Santa Barbara and Ventura counties. Even currently casual taxa have a potential long-term impact because, unlike many kinds of environmental pollutants that are eventually neutralized within or disappear from the system upon termination of the source, biological pollutants such as naturalizing non-native plants are self-perpetuating, often increasing in prominence and distribution with time

regardless of whether the source has been terminated (O'Kennon et al. 1999). Moreover, as stated above, the cost of control rises linearly as population size increases (Bayer 1999; Rejmanek 2000); because populations often enlarge logarithmically, ultimate control costs for populations left uncontrolled may exceed available resources. As a result, awareness of the identity and ecology of a potential or incipient weed population is not only important, it is also economically imperative—if control or eradication are eventual goals.

We hope that this compilation will spur two activities: first, further exploration for non-native spontaneous plants in California; and second, clarification of the current status of the taxa on this list, especially those classified as "No Current Information (NCI)". Clearly, the disturbed areas on which many of these latter taxa established in the earlier decades of this century have subsequently been stabilized by parking lots or other intensive development; however, other populations may have expanded their range, but are on private land no longer readily accessible.

*On-going need for vouchered reports.* The present compilation is not exhaustive for several reasons. First and foremost is the rapid rate at which new weedy taxa are being found in a state as large and geographically diverse as California. Secondly, a compilation such as this, which includes many records known only from obscure locations or single sites in California, comprises a major effort by botanical collectors of modern and previous eras; without their past and ongoing efforts this collation would not exist. With this in mind, as California's increase in human population and consequent plant introductions continues, it is important that the collection and documentation of non-native taxa, by the submission of specimens to public collections, continue as well.

As a final note we wish to again emphasize the absolute need for specimen documentation of new reports of spontaneous non-native plants (see Dean and Hrusa 2000 for instructions on collecting and documenting plant occurrences). The fact that determining and verifying these species does not keep pace with the introduction rate is largely a reflection of the difficulty in applying names to plants whose geographic origins are not known and which may be cultivated forms or which have become phenetically modified in their new habitats. For this reason it has been discouraging to realize how many seemingly authoritative reports, via both agencies and private organizations, lack confirming specimen material. Indeed, some lacked even the documentation of who applied the name and when, or where the plant was reported to grow. Without such information a reliable understanding of which taxon is actually represented is not possible. The ramifications of this information gap are great; ecological behavior, environmental tolerances, devel-

opmental and phenological patterns are often species-specific, and control measures, whether physical, chemical, or biological, may not be effective if the totality of life history is not correctly understood. The essential first step toward accessing whatever critical information is available is having an accurate identification (for a case study, see Thomas and Room 1986).

The addition of so many non-native pest plants with the potential for becoming naturalized further underscores just how much the weed invasion of California should be of continuing economic and ecological concern. The current catalogue, while the result of intensive research in both the field and herbarium, is by no means complete; rather it serves to point out the extent to which non-native plants must be constantly sought out and reported.

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## APPENDIX 1

## LIST OF TAXA WITH NATURALIZATION CLASS

List of non-native vascular plant taxa occurring spontaneously in California but not included in *The Jepson Manual*. Organization as in the *Manual*. **Current Status** subcategories in parentheses: NW = naturalized in wildlands, N = naturalized (outside of wildlands), TEN = persistence tenuous, C = casual (waif), GH/C = greenhouse/cultivation, EXT = extirpated. See Table 1 and Appendix 2.

## FERNS AND ALLIES

## Salviniaceae

*Salvinia molesta* D.S. Mitch., (NW).

## Selaginellaceae

*Selaginella kraussiana* (Kunze) A. Braun, (N).

## Ephedraceae

*Ephedra altissima* Desf., (NCI).

*Ephedra distachya* L., (NW).

## CONIFERS

## Pinaceae

*Pinus halepensis* P. Mill., (N).

*Pinus pinea* L., (NW).

## ANGIOSPERMS: DICOTS

## Acanthaceae

*Acanthus mollis* L., (C).

## Aceraceae

*Acer campestre* L., (N).

*Acer saccharinum* L., (NW).

## Aizoaceae

*Galenia pubescens* (Ecklon & Zeyher) Druce var. *pubescens*, (N).

## Amaranthaceae

*Amaranthus blitum* L. subsp. *emarginatus* (Uline & Bray) Carretero, (C).

*Amaranthus rudis* Sauer, (N).

*Braylinea densa* (Willd.) Small, (NCI).

*Froelichia gracilis* (Hook.) Moq., (NCI).

## Anacardiaceae

*Rhus lancea* L.f., (N).

*Schinus polygamus* (Cav.) Cabr., (N).

## Apocynaceae

*Nerium oleander* L., (NW).

## Aquifoliaceae

*Ilex* × *attenuata* Ashe, (NCI).

## Araliaceae

*Hedera canariensis* Willd., (NW).

## Asclepiadaceae

*Asclepias fruticosa* L., (C).

*Calotropis procera* (Ait.) Ait. f., (C).

*Cynanchum louiseae* Kartesz & Gandhi, (N).

## Asteraceae

*Achillea filipendulina* Lam., (NCI).

*Artemisia vulgaris* L. *sensu stricto*, (NCI).

*Aster novae-angliae* L., (NCI).

*Carthamus oxyacantha* M. Bieb., (C).

*Centaurea babylonica* L., (C).

*Chrysanthemum balsamita* L., (C).

*Cirsium scabrum* (Poir.) Bonnett & Barratte, (NCI).

*Coreopsis grandiflora* Hogg. ex Sweet, (C).

*Cotula mexicana* (DC.) Cabrera, (N).

*Crepis tectorum* L., (N).

*Dendranthema* × *grandiflorum* Kitam., (NCI).

*Dittrichia graveolens* (L.) Greuter, (NW).

*Emilia fosbergii* D.H. Nicolson, (GH/C).

*Emilia sonchifolia* (L.) DC. ex Wight, (GH/C).

*Grindelia papposa* Nesom & Suh, (NCI).

*Helianthus tuberosus* L., (C).

*Helichrysum petiolare* Hilliard & B. L. Burt., (NW).

*Heliomeris multiflora* Nutt. *multiflora*, (TEN).

*Helipterum roseum* (Hook.) Benth., (NCI).

*Lasiospermum bipinnatum* (Thunb.) Druce, (NW).

*Leontodon muelleri* (Schultz-Bip.) Fiori, (NCI).

*Oncosiphon piluliferum* (L.f.) Kallersjo, (N).

*Osteospermum fruticosum* (L.) Norl., (NW).

*Pericallis cruenta* (DC. non Roth) Webb. & Berth., (NCI).

*Porophyllum ruderales* (Jacq.) Cass., (C).

*Ratibida columnifera* (Nutt.) Wooton & Standl., (NCI).

*Senecio squalidus* L., (NCI).

*Tragopogon hybridus* L., (NCI).

*Tripleurospermum maritimum* (L.) W. D. J. Koch, (TEN).

## Balsaminaceae

- Impatiens balfourii* J.D. Hook., (N).  
*Impatiens noli-tangere* L., (N).

## Berberidaceae

- Berberis darwinii* Hook., (NCI).

## Betulaceae

- Alnus cordata* (Loisel.) Duby, (C).

## Bignoniaceae

- Campsis radicans* (L.) Bureau, (TEN).  
*Catalpa bignonioides* Walter, (NW).

## Boraginaceae

- Echium lusitanicum* L., (TEN).  
*Pentaglottis sempervirens* (L.) Tausch ex Bailey, (NCI).

## Brassicaceae

- Brassica fruticulosa* Cyrillo, (N).  
*Cardamine flexuosa* With., (N).  
*Coincya monensis* (L.) Greuter & Burdet, (NW).  
*Iberis umbellata* L., (C).  
*Rorippa sylvestris* (L.) Besser, (TEN).

## Cabombaceae

- Cabomba caroliniana* A. Gray, (NW).

## Campanulaceae

- Campanula medium* L., (C).  
*Lobelia erinus* L., (C).

## Caprifoliaceae

- Leycesteria formosa* Wallich., (NCI).  
*Viburnum tinus* L., (NCI).

## Caryophyllaceae

- Silene pseudotocion* Desf., (NCI).

## Celastraceae

- Maytenus boaria* Molina, (NW).

## Chenopodiaceae

- Atriplex muelleri* Benth., (NCI).  
*Chenopodium watsonii* A. Nels., (NCI).  
*Salsola kali* L. subsp. *pontica* (Pallas) Mosyakin, (NCI).

## Cistaceae

- Halimium lasianthum* (Lam.) Spach, (NCI).

## Convolvulaceae

- Calystegia silvatica* (Kit.) Griseb. subsp. *disjuncta* Brummitt, (N).  
*Convolvulus tricolor* L., (NCI).  
*Dichondra micrantha* Urb., (NCI).  
*Ipomoea aquatica* Forssk., (C).  
*Ipomoea lacunosa* L., (C).  
*Ipomoea quamoclit* L., (C).

## Crassulaceae

- Crassula multicava* Lem., (NW).  
*Sedum album* L., (N).  
*Sedum dendroideum* Sesse & Moc. ex DC., (NCI).

## Cucurbitaceae

- Cucumis anguria* L., (NCI).  
*Cucurbita ficifolia* Bouche, (NCI).  
*Cucurbita pepo* L. var. *medullosa* Alef., (C).

## Cuscutaceae

- Cuscuta reflexa* Roxb., (EXT).

## Droseraceae

- Drosera aliciae* Hamet, (NCI).  
*Drosera capensis* L., (NCI).  
*Drosera tracyi* MacFarlane, (NW).

## Ebenaceae

- Diospyros virginiana* L. var. *virginiana*, (NW).

## Elaeocarpaceae

- Aristotelia chilensis* (Molina) Stuntz, (TEN).  
*Muntingia calabura* L., (GH/C).

## Escalloniaceae

- Escallonia macrantha* Hook. & Arn., (NCI).

## Euphorbiaceae

- Euphorbia characias* L., (NCI).  
*Euphorbia cyathophora* Murr., (NCI).  
*Euphorbia dendroides* L., (NW).  
*Euphorbia heterophylla* L., (NCI).  
*Euphorbia hirta* L., (N).  
*Euphorbia hypericifolia* L., (GH/C).  
*Euphorbia marginata* Pursh, (NCI).  
*Euphorbia myrsinites* L., (NCI).  
*Euphorbia rigida* M. Bieb., (NCI).  
*Euphorbia terracina* L., (NW).  
*Sapium sebiferum* (L.) Roxb., (NW).

## Fabaceae

- Astragalus cicer* L., (TEN).  
*Cassia nemophila* A. Cunn., (TEN).  
*Ceratonlia siliqua* L., (NW).  
*Coronilla valentina* L., (NW).  
*Dolichos lignosus* Pers., (NCI).  
*Genista monosperma* (L.) Lam, non Link, nec Del., (NW).  
*Gleditsia triacanthos* L., (NW).  
*Lathyrus sativus* L., (C).  
*Ononis alopecuroides* L., (NW).  
*Robinia hispida* L., (N).  
*Senna artemisioides* (Gaudich. ex DC.) Randell, (N).  
*Senna obtusifolia* (L.) H.S. Irwin & Barneby, (N).  
*Sesbania punicea* (Cav.) Benth, (N).  
*Trifolium alexandrinum* L., (NCI).  
*Trifolium cernuum* Brot., (N).  
*Trifolium gemellum* Poir. ex Willd., (N).  
*Trifolium resupinatum* L., (NCI).  
*Trifolium retusum* L., (NW).  
*Trifolium stellatum* L., (NCI).  
*Trifolium striatum* L., (NCI).  
*Trifolium tomentosum* Willk. ex Nyman, (NW).

*Trifolium vesiculosum* Savi, (N).  
*Trigonella corniculata* L., (NCI).  
*Trigonella foenum-graecum* L., (NCI).  
*Vicia bithynica* (L.) L., (NCI).

## Fagaceae

*Quercus ilex* L., (N).

## Geraniaceae

*Geranium columbinum* L., (NCI).  
*Geranium lucidum* L., (N).  
*Geranium purpureum* Vill., (NW).  
*Geranium pyrenaicum* Burm. f., (C).  
*Geranium rotundifolium* L., (NW).  
*Geranium texanum* (Trel.) A. Heller, (NCI).

## Hamamelidaceae

*Liquidambar styraciflua* L., (TEN).

## Hydrophyllaceae

*Wigandia caracasana* HBK., (NCI).

## Hypericaceae

*Hypericum androsaemum* L., (N).  
*Hypericum calycinum* L., (TEN).  
*Hypericum hookerianum* Wight & Arn., (TEN).

## Lamiaceae

*Calamintha sylvatica* Bromf. subsp. *ascendens* (JordaN).  
 P.W. Ball, (TEN).  
*Cedronella canariensis* (L.) Willd. ex Webb & Berth.,  
 (NCI).  
*Galeopsis tetrahit* L., (NCI).  
*Lamium galeobdolon* (L.) Ehrend. & Polatsch., (TEN).  
*Lavandula stoechas* L., (C).  
*Mentha* × *villosa* Huds., (NCI).  
*Monarda citriodora* Cerv., (N).  
*Rosmarinus officinalis* L., (C).  
*Salvia longistyla* Benth., (N).  
*Salvia microphylla* Benth., (NCI).  
*Salvia reflexa* Hornem., (GH/C).  
*Salvia virgata* Jacq., (NCI).  
*Scutellaria caerulea* M. & S., (C).  
*Stachys floridana* Shuttlew., (GH/C).

## Lauraceae

*Cinnamomum camphora* (L.) J. Presl, (C).  
*Laurus nobilis* L., (TEN).

## Lentibulariaceae

*Utricularia subulata* L., (NCI).

## Limnanthaceae

*Limnanthus macounii* Trel., (N).

## Linaceae

*Linum trigynum* L., (NCI).

## Malvaceae

*Anisodonteia capensis* (L.) Bates, (C).  
*Anoda pentaschista* A. Gray, (NCI).  
*Gossypium hirsutum* L., (NCI).

*Hoheria populnea* A. Cunn., (NCI).  
*Lavatera olbia* L., (NCI).  
*Lavatera trimestris* L., (NCI).  
*Malva verticillata* L., (NCI).  
*Sida spinosa* L., (NCI).

## Moraceae

*Fatoua villosa* (Thunb.) Nakai, (GH/C).  
*Ficus palmata* Forssk., (NCI).

## Nymphaeaceae

*Nymphaea alba* L., (NCI).

## Oleaceae

*Fraxinus uhdei* (Wenz.) Lingel., (NW).  
*Ligustrum lucidum* W.T. Aiton, (NW).  
*Ligustrum ovalifolium* Hassk., (NW).  
*Olea africana* Mill., (TEN).

## Onagraceae

*Fuchsia magellanica* Lam., (NW).  
*Fuchsia* × *hybrida* Voss., (NCI).

## Orobanchaceae

*Orobanche hederæ* Duby, (TEN).

## Papaveraceae

*Fumaria capreolata* L., (N).  
*Papaver* × *hybridum* L., (NCI).

## Passifloraceae

*Passiflora caerulea* L., (N).  
*Passiflora manicata* (Juss.) Pers., (NCI).  
*Passiflora mixta* L. f., (N).  
*Passiflora tarminiana* Coppens & Barney, (N).

## Pedaliaceae

*Sesamum indicum* L., (C).

## Plumbaginaceae

*Limonium ramosissimum* (Poir.) Maire subsp. *provinciale*  
 (Pignatti) Pignatti, (NW).

## Polygalaceae

*Polygala myrtifolia* L., (NCI).

## Polygonaceae

*Polygonum multiflorum* Thunb., (GH/C).  
*Polygonum orientale* L., (C).

## Ranunculaceae

*Caltha palustris* L., (NW).  
*Clematis terniflora* DC., (TEN).  
*Clematis vitalba* L., (NCI).  
*Nigella damascena* L., (N).  
*Ranunculus cortusifolius* L., (TEN).

## Rhamnaceae

*Ziziphus jujuba* L., (C).

## Rosaceae

- Cotoneaster lacteus* W.W. Smith (NW).  
*Crataegus monogyna* Jacq., (NW).  
*Cydonia oblonga* Mill., (NCI).  
*Cydonia sinensis* Thoun., (NCI).  
*Eriobotrya japonica* Lindl., (NCI).  
*Filipendula vulgaris* Moench, (NCI).  
*Photinia davidsoniae* Rehd. & Wilson, (NCI).  
*Potentilla anglica* Laicharding, (NW).  
*Potentilla reptans* L., (TEN).  
*Prunus laurocerasus* L., (NW).  
*Prunus persica* (L.) Batsch, (C).  
*Prunus serrulata* Lindl., (C).  
*Pyracantha coccinea* M. Roem., (TEN).  
*Pyracantha crenatoserrata* (Hance) Rehder, (N).  
*Pyracantha crenulata* (D. DoN). M. Roem., (TEN).  
*Pyrus communis* L., (N).  
*Rosa multiflora* Thunb. ex Murray, (NCI).  
*Rubus ulmifolius* Schott var. *ulmifolius*, (N).

## Rubiaceae

- Coprosma repens* A. Rich., (N).

## Salicaceae

- Populus nigra* L. cv. "Italica", (TEN).

## Sarraceniaceae

- Sarracenia* aff. *rubra* Walter, (N).

## Scrophulariaceae

- Anarrhinum bellidifolium* (L.) Willd., (C).  
*Limnophila* × *ludoviciana* Thieret, (TEN).  
*Mazus japonicus* Kuntze, (GH/C).  
*Penstemon strictus* Benth., (TEN).  
*Penstemon subglaber* Rydb., (TEN).  
*Scrophularia peregrina* L., (N).  
*Verbascum olympicum* Boiss. non Bunyard, (NW).

## Solanaceae

- Atropa belladonna* L., (NCI).  
*Capsicum annuum* L., (NCI).  
*Cestrum parqui* L'Her., (NCI).  
*Lycium ferocissimum* Meirs, (NCI).  
*Nicotiana* × *sanderiae* Hort. ex Wats., (C).  
*Nicotiana tabacum* L., (C).  
*Petunia violacea* Lindl., (NCI).  
*Solanum gayanum* (Remy) Phil. f., (NCI).  
*Solanum scabrum* Mill., (C).  
*Solanum villosum* Mill., (C).

## Urticaceae

- Boehmeria cylindrica* (L.) Sw., (NW).  
*Laportea aestuans* (L.) Chew, (GH/C).

## Verbenaceae

- Verbena rigida* Spreng., (NCI).  
*Vitex agnus-castus* L., (NCI).

## Vitaceae

- Cissus antarctica* Venten., (NCI).  
*Vitis aestivalis* Michx., (NCI).  
*Vitis rupestris* Scheele, (TEN).

## Zygophyllaceae

- Peganum harmala* L., (EXT).

## ANGIOSPERMS—MONOCOTS

## Alismataceae

- Sagittaria brevirostra* Mackenzie & Bush, (NCI).  
*Sagittaria rigida* Pursh, (NW).

## Araceae

- Arum palestinum* Boiss., (TEN).  
*Dracunculus vulgaris* Schott, (N).  
*Pinellia ternata* (Thunberg) Makino, (NCI).

## Cyperaceae

- Bulbostylis barbata* Kunth, (GH/C).  
*Cyperus flavescens* L., (NW).  
*Cyperus flavicomus* Michx., (N).  
*Cyperus gracilis* R. Br., (NCI).  
*Cyperus iria* L., (TEN).  
*Cyperus owanii* Boeck, (NCI).  
*Cyperus papyrus* L., (NCI).  
*Fimbristylis autumnalis* (L.) Roem. & Schult., (NW).  
*Scirpus cyperinus* (L.) Kunth, (NW).  
*Scirpus prolifer* Rottb., (NCI).

## Eriocaulaceae

- Eriocaulon cinereum* R. Br., (EXT).

## Hydrocharitaceae

- Limnobia laevigata* (Humb. & Bonpl. ex Willd.) Heine, (NW).

## Iridaceae

- Iris foetidissima* L., (N).  
*Iris germanica* L., (TEN).  
*Iris orientalis* L., (NCI).  
*Ixia polystachya* L., (NCI).  
*Ixia speciosa* Andrews, (NCI).  
*Moraea collina* Thunb., (N).  
*Moraea polystachya* Ker Gawl., (NCI).

## Juncaceae

- Juncus nodatus* Cov., (N).

Liliaceae (*sensu lato*)

- Agapanthus praecox* Willd., (NCI).  
*Allium cepa* L., (NCI).  
*Allium sativum* L., (C).  
*Amaryllis belladonna* L., (TEN).  
*Chlorophytum capense* (L.) Druce, (C).  
*Hyacinthus orientalis* L., (C).  
*Kniphofia uvaria* (L.) Hooker, (NW).  
*Leucojum aestivum* L., (NCI).  
*Narcissus pseudonarcissus* L., (NW).  
*Narcissus tazetta* L., (NW).  
*Ornithogalum umbellatum* L., (GH/C).  
*Pancratium maritimum* L., (N).  
*Tulipa clusiana* DC. in Redoute, (TEN).

## Poaceae

- Acrachne racemosa* (Roem. & Schult.) Ohwi, (TEN).  
*Aira caryophyllea* L. var. *cupaniana* (Guss.) Fiori, (NCI).

*Amphibromus neesii* Steud., (NW).  
*Aristida dichotoma* Michx., (NW).  
*Chloris truncata* R. Br., (N).  
*Echinochloa crusgalli* subsp. *spiralis* (Vasing.) Tzvelev, (N).  
*Echinochloa esculenta* (A. Br.) H. Scholz, (NCI).  
*Ehrharta longiflora* Sm., (NW).  
*Eragrostis curvula* (Schräd.) Nees var. *conferta* Nees, (N).  
*Eremochloa ciliaris* (L.) Merr., (EXT).  
*Gaudinia fragilis* (L.) P. Beauv., (NW).  
*Glyceria fluitans* (L.) R. Br., (NW).  
*Hordeum vulgare* L. *sensu lato*, (C).  
*Leptochloa dubia* (Kunth) Nees, (N).  
*Nassella tenuissima* (Trin.) Barkworth, (C).  
*Panicum maximum* Jacq., (GH/C).  
*Panicum repens* L., (NCI).  
*Panicum rigidulum* Bosc ex Nees var. *rigidulum*, (NCI).  
*Panicum texanum* Buckl., (TEN).  
*Pennisetum glaucum* (L.) R. Br., (C).  
*Pennisetum latifolium* Spreng., (NCI).  
*Phalaris coerulescens* Desf., (C).  
*Phyllostachys aurea* A. & C. Riviere, (NCI).  
*Phyllostachys bambusoides* Siebold & Zuccarini, (NCI).  
*Piptochaetium stipoides* Hackel ex Arech. *sensu lato*, (NW).  
*Polypogon imberbis* (Phil.) Bjorkm., (NCI).  
*Pseudosasa japonica* (Sieb. & Zucc. ex Steud.) Makino ex Naka, (NCI).  
*Schedonnardus paniculatus* (Nutt.) Trel., (NCI).  
*Spartina anglica* C.E. Hubb., (NW).  
*Stipa capensis* Thunb., (NW).  
*Themeda quadrivalvis* (L.) Kuntze, (TEN).  
*Tribolium obliterum* (Hemzl.) Renvoize, (NW).  
*Triticum aestivum* L., (C).

#### Pontederiaceae

*Heteranthera rotundifolia* (Kunth) Griseb., (N).

#### APPENDIX 2

##### ANNOTATED CATALOGUE

Family circumscriptions and organization follow *The Jepson Manual*. Generic and specific applications reflect published treatments by specialists, modified only if clearer information was gained by utilizing an alternative nomenclature. Abbreviations are as follows: **DISTRIBUTION** (DIST) with geographic subdivisions as used in *The Jepson Manual*; **CURRENT STATUS** (CS); Current Status subcategories: NATURALIZED IN WILDLANDS (NW); NATURALIZED (OUTSIDE OF WILDLANDS) (N); PERSISTENCE TENUOUS (TEN); CASUAL (waif) (C); GREENHOUSE/CULTIVATION (GH/C); EXTIRPATED (EXT); **DOCUMENTATION** (DOC). For details and descriptions of these categories see Tables 1 and 2.

#### FERNS AND ALLIES

##### Salviniaceae

*Salvinia molesta* D.S. Mitch.: **DIST**: CCo, DSon, SCo: **CS**: NW, N (DSon), TEN (SCo): **DOC**: **Imperial Co.**: N side Hwy 98 in E Highline Canal nr. Winterhaven. T16S, R20E, Sec. 01, SB. Aug. 25, 1999, *Johnson s.n.* (CDA); All American Canal at Drop 1 nr. Coachella Canal. Sample from equipment which at this point collects vegetation floating down the canal. Winterhaven area. T16S, R20E, Sec. 31, SB. Aug. 25, 1999, *Johnson s.n.* (CDA); **Riverside Co.**: Drain canal of Palo Verde Irrig. District, Blythe

region. T06S, R23E, SB. Aug. 20, 1999, *R. O'Connell s.n.* (CDA); **San Diego Co.**: Private pond in vicinity of Fallbrook off Harris Truck trail. Oct. 28, 1999, *S. Riviera s.n.* (CDA); **San Luis Obispo Co.**: Private pond off Price Cyn. Rd. T30S, R12E, MD. Nov. 27, 2001, *S. Stoltz s.n.* (CDA, OBI); **NOTES**: Reported from San Diego River (San Diego Co.) Aug., 1999 but no specimen has been seen. Fallbrook location may have been purposely planted for increase and resale. Eradication attempts are currently underway by CDFA, USDA-APHIS in all sites. A Federal Noxious Weed, sale or growth is prohibited.

##### Selaginellaceae

*Selaginella kraussiana* (Kunze) A. Braun: **DIST**: NCo: **CS**: N: **DOC**: **Humboldt Co.**: Arcata. Damp, shaded areas near Humboldt State University Conservatory. April 5, 2000, *G. Leppig 1286* (HSC); redwood forest behind Humboldt State University, along stream at Fern Lake. April 12, 2000, *G. Leppig 1290* (CDA, HSC); **Sonoma Co.**: Best, C., et al. (1996, pg. 25).

##### Ephedraceae

*Ephedra altissima* Desf.: **DIST**: SCo: **CS**: NCI: **DOC**: **San Diego Co.**: Spreading from root shoots and climbing to 7 m to top of adjacent macadamia tree, site of old USDA Exp. Station, N of Science Park Dr., E of North Torrey Pines Rd, N of La Jolla. T15S, R04W, Sec. 01, SB. Oct. 1, 1974, *T.C. Fuller 20049* (CDA).

*Ephedra distachya* L.: **DIST**: SCo: **CS**: NW: **DOC**: **Santa Barbara Co.**: Smith, C.F. (1998, pg. 372): **NOTES**: Reported as 'established' in Smith (1998), but by our criteria Wilken (SBBG) reports that it is naturalized in the oak woodlands about the Trout Club in the Santa Ynez Mtns. (pers. comm.). Det. by D. Wilken, verified also by S. Carlquist (SBBG).

#### CONIFERS

##### Pinaceae

*Pinus halepensis* P. Mill.: **DIST**: CCo, SnFrB: **CS**: N: **DOC**: **Contra Costa Co.**: Mount Diablo, W slope Mount Zion, upper extent of Kaiser quarry reddish chert-like rocks on steep 25% W facing slope; mature trees (planted in rows), with abundant reproduction, juveniles to 10 ft tall. Elev. 1550 ft, T01N, R01W, Sec. 22, MD. Oct. 9, 1996, *D.W. Taylor 15896* (UC); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 62): **NOTES**: Seedlings are occasionally encountered about cultivated trees but are seldom allowed to mature.

*Pinus pinea* L.: **DIST**: n ChI, SnFrB: **CS**: naturalized: **DOC**: **Contra Costa Co.**: Walnut Creek, Lakewood subdivision, on hillside. June 21, 1950, *W.S. Malloch s.n.* (UC); **Santa Barbara Co.**: Junak, S. et al. (1995, pg. 64).

#### ANGIOSPERMS—DICOTS

##### Acanthaceae

*Acanthus mollis* L.: **DIST**: SnFrB: **CS**: C: **DOC**: **San Mateo Co.**: McClintock, E., et al. (1990, pg. 63): **NOTES**: Probably originating via garden waste; individuals sites often long-persistent, but permanence tenuous.

##### Aceraceae

*Acer campestre* L.: **DIST**: SnFrB: **CS**: N: **DOC**: **Alameda Co.**: lower Strawberry Canyon firetrail behind UC Berkeley campus, a few small trees at edge of woodland,



June 11, 1998, *B. Ertter & A. Rusev 16152* (UC): **NOTES:** Verbal reports indicate it may be sparingly naturalized elsewhere in the East Bay Hills.

*Acer saccharinum* L.: **DIST:** ScV: **CS:** NW: **DOC:** **Glenn Co.:** Sacramento River at Butte City boat launch site, small tree on silty river bank. Oct. 22, 1998, *Ertter 16448* (UC); Bank btwn. levee and W side of Butte Creek approx. ½ mi NE of confluence with Howard Slough, and immed. below McPherrin Dam (private and scheduled for removal). Two multi-trunked trees,  $\pm$  12 meters tall, both apparently sterile, possibly persisting from old plantings. 39°27'N; 121°53'W. Sept. 6, 1996, *G.F. Hrusa 13571* (CDA); **Sacramento Co.:** Sacramento River in Sacramento to near the end of 10th St., elev. 85 ft. Apr. 28, 1997, *D. Kelch DGK97.012* (UC); Betw. N side American River and William Pond, American River Parkway at Arden Way entrance. 38°33'N; 121°22'W. June 28, 1998, *B. Meyers-Rice MR980601* (CDA, DAV); N bank American River, American River Parkway, few hundred meters downriver of the Estates Dr. entrance. June 28, 1998, *B. Meyers-Rice MR980602* (DAV); American River Recreation Trail, E of Union Pacific trestle. T07N, R05E, Sec. 31, MD. April 13, 1984, *G.D. Barbe 4142* (CDA, DAV).

#### Aizoaceae

*Galenia pubescens* (Ecklon & Zeyher) Druce var. *pubescens*: **DIST:** SCo: **CS:** N: **DOC:** **Los Angeles Co.:** Ross, T. (1993, pg. 226–228); Ross, T. and S. Boyd (1996, pg. 432–433); **Riverside Co.:** U.S. Forest Fire Lab, Cyn. Crest Dr. El. 1200 ft. Fairly common in experimental planting of *Artemisia californica*, *Eriogonum fasciculatum* etc., Doubtless progeny of plants grown by E.C. Nord in 1970. Aug. 9, 1996, *J. Beyers s.n.* (UCR); **NOTES:** A specimen from **San Diego Co.** at UCR has not yet been accessioned.

#### Amaranthaceae

*Amaranthus blitum* L. subsp. *emarginatus* (Uline & Bray) Carretero: **DIST:** SCo: **CS:** C: **DOC:** **Los Angeles Co.:** waste ground at intersection of Beach Blvd. (Hwy 39) and Rosecrans Ave., at the Orange County line, La Mirada. Oct. 29, 1988, *T. Yutani s.n.* (CDA); Solitary small weed in a potted plant purchased at The Farm Store, Cal Poly Pomona. Jan. 10, 2002, *A.C. Sanders 24891* (UCR); **Riverside Co.:** Moreno Valley, weed in unintended planter beside Home Depot at Pigeon Pass Rd. and Hwy 160. Nov. 25, 2001, *A.C. Sanders 24887* (UCR); **NOTES:** Determination by S. Mosyakin (KW, Mar. 2001), [= *A. blitum* subsp. *polygonoides* (Moq.-Tandon) Carretero]. See Costea et al. (2001) for taxonomic discussion. Occasionally intercepted during nursery stock inspections on material from the US southeast, esp. Florida. Adapted to tropical and subtropical climates, this species would not be expected to be more than a minor or casual weed of greenhouse, garden or nursery. Sometimes treated (and reported) as *A. lividus* L.

*Amaranthus rudis* Sauer: **DIST:** SCo, ScV: **CS:** N: **DOC:** **Butte Co.:** E side Sac. R. NW Parrott Landing, 1 mi. SE Ord Ferry, 12 mi. SW Chico. Riparian woodland. Sept. 21, 1999, *L. Ahart 8267, 8266* (CDA, CHSC); 6 mi. W Chico, gravel bar, Sac. R. Sept. 26, 1981, *L. Ahart 3205* (CAS, CDA, CHSC), det. by J.T. Howell 12/81; **Sacramento Co.:** NW corner Int. US 50 and Howe Ave., Sacramento. Single plant. Sept. 22, 1985, *A. Shapiro s.n.* (CDA, DAV); **Santa Barbara Co.:** SPRR, Carpenteria. Sept. 5, 1957, *H.M. Pollard* (CAS, CDA), det. J. Sauer 5-1959 (as *A. tamariscinus* Nutt.); SPRR yards, Santa Bar-

bara. Sept. 26, 1957, *H.M. Pollard s.n.* (CAS, CDA), det. J. Sauer 5/1959; loc. cit. Oct. 8, 1957, *H.M. Pollard s.n.* (DAV), det. J. Sauer 2/1974; SPRR yards, Santa Barbara. Oct. 8, 1957, *H.M. Pollard s.n.* (DAV); **NOTES:** Similar among dioecious California *Amaranthi* to *A. arenicola*. Pistillate plants readily distinguished among the California taxa by their two, rather than five pistillate sepals. Staminate plants of *A. rudis* have acute to acuminate sepal tips in contrast to the obtuse to retuse sepal tips in *A. arenicola*. *Amaranthus tamariscinus* Nutt. misapplied. Staminate and pistillate plants comprising *Townsend s.n.*, Aug. 2, 1968, (CDA, RSA) collected nr. Pala in San Diego Co. and the source of the citation for *A. tamariscinus* in Munz (1974) USDA. NRCS (2001) and Beauchamp (1986), are, acc. to Hrusa, misidentified *A. palmeri* S. Wats.

*Braylinea densa* (Willd.) Small: **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Howell, J.T. (1966, pg. 256); **NOTES:** Probably a roadside casual, not since reported in California.

*Froelichia gracilis* (Hook.) Moq.: **DIST:** SCo: **CS:** NCI: **DOC:** **Los Angeles Co.:** Santa Fe RR, San Dimas. June 23, 1955, *G.W. Garrettson s.n.* (CDA). Det. by P.A. Munz.

#### Anacardiaceae

*Rhus lancea* L.f.: **DIST:** SCo, DSo: **CS:** N: **DOC:** **Riverside Co.:** Coachella Valley, Palm Springs, W side of Palm Canyon Dr. just above (S of) junction with Hwy 111, weedy disturbed vacant lot, clearly spontaneous. 33°47.75'N, 116°32.52'W; T04S, R04E, Sec. 27, SB. El. 140 m. Mar. 17 1996, *A. C. Sanders and G. Helmkamp 17982* (UCR); Palm Springs, Murray Canyon, off Palm Canyon, a solitary arborescent shrub 4–5 m tall at the edge of the stream between palm groves, elev. 245 m, far from any cultivated plants, 33°45.5'N, 116°33'W, T04N, R03E, Sec. 10, SB. Feb 8, 1997, *A. C. Sanders et al 19686* (UCR); **Riverside, S side of the U.C.R. campus,** a solitary shrub, apparently spontaneous, growing wedged between a large pecan tree and the wall of a concrete reservoir. Elev. 400 m. Feb 26, 1997, *A. C. Sanders 19688* (UCR); **Ventura Co.:** Hills north of Moorpark, 0.5 mile west of Happy Camp Canyon, 1.9 miles north of Arroyo Simi Channel, T02N R19W sec. 33, elev. 245–275 m, invasive in coastal sage scrub, particularly in small drainages. Jul. 27, 1995, *C. Jones and R. Ramirez 8* (RSA, UCR); **NOTES:** Native to S. Africa and widely cultivated in California, these are the first records of naturalized plants in California. Doubtless naturalized elsewhere in S. Calif. as the locations where it has been found represent much of the range of environmental conditions in lowland southern California, from the Sonoran Desert to the mild maritime influenced climate of Ventura County.

*Schinus polygamus* (Cav.) Cabr.: **DIST:** SCo: **CS:** N: **DOC:** **Los Angeles, Riverside, San Bernardino Cos.:** Sanders, A.C. (1996, pg. 530); **NOTES:** Widespread in urban So. Calif., but is widely ignored by collectors. Still scarce in  $\pm$  natural areas, but often encountered in disturbed sites.

#### Apocynaceae

*Nerium oleander* L.: **DIST:** SCo, ScV: **CS:** NW: **DOC:** **Los Angeles Co.:** San Gabriel Mtns., in and near Glendora Wilderness Park, Harrow Canyon at the third debris basin. Elev. 1450 ft, Jul. 14, 1989, *D. Swinney s.n.* (UCR); **Riverside Co.:** Temple, P.J. (1999, pg. 55); **San Bernardino Co.:** Waterman Canyon Road at old Arrowhead Hot

Springs Resort, 7 km north Hwys 30 and 18 intersection. Sandy/rocky riparian with *Artemisia californica* and *Vitis girdiana*, May 9, 1972, *E. Trubschenck* 28 (UCR); Waterman Canyon, 1 km W of the old Arrowhead Hot Springs Hotel, 117°16'W, 34°11.5'N, T01N, R04W, Sec. 11, SB. Elev. 1900 ft, abundant shrub in moist areas along the rocky canyon bottom along creek, numerous seedlings and plants of all sizes. Apr. 27, 1993, A. C. Sanders *et al.* 13824 (UCR); along Colorado River north of Parker Bridge, T01N, R26E, Secs. 17 and 18, SB. Elev. 350 ft, mostly alkali and disturbed sites. May 2, 1978, *Faulkner* 572 (UCR).: **Shasta Co.**: Keeley, J., (1992, pg. 157): **NOTES**: Naturalized at the Waterman Canyon site for at least 30 years. Plants are abundant there, forming large thickets along the creek and obviously reproducing sexually. There is considerable variation in flower color, including shades of pink never seen in cultivation. Also established in nearby Hot Springs and Strawberry Canyons. The Swinney collection certainly represents a naturalized population as it shows (dried, no color notes) the mottled pink flower color that is common in the reproducing population at Waterman Canyon. The Faulkner collection might be questioned because the dried flowers appear to be the pure white which is common in cultivated plants. There is nothing on the label which indicates that this collection was from cultivated or persisting plants, but there also is nothing eliminating that possibility. This report needs confirmation.

#### Aquifoliaceae

*Ilex × attenuata* Ashe: **DIST**: ScV: **CS**: NCI: **DOC**: **Sacramento Co.**: Volunteer tree on creek bank. Hoffman Lane, Fair Oaks. Jan. 30, 1977, *Bly s.n.* (CDA).

#### Araliaceae

*Hedera canariensis* Willd. (incl. *H. algeriensis* Hibb.): **DIST**: CCo, SCo, SnBR, SnFrB, SnGB: **CS**: NW: **DOC**: **Alameda Co.**: Albany Hill, abundant in oak forest. Jan. 14, 1995, *B. Ertter* 13918 (UC); **Orange Co.**: Trabuco Canyon. May 13, 1966, *E.W. Lathrop* 6297 (UCR); **San Bernardino Co.**: upper Waterman Canyon, San Bernardino Mtns. Dec. 23, 1998, A.C. Sanders 22369 (UCR); Dick Stoddard Canyon, San Gabriel Mtns. Jan. 15, 1994, *Swinney* 2695 (UCR); **NOTES**: Differs from *H. helix* in having larger leaves with fewer (most often only 3), more rounded lobes and fainter veins; more robust stems that are more shallowly rooted at the nodes; and rusty hairs on the growing tips that are basally fused into tightly appressed, stellate-peltate trichomes (vs. white and ± spreading in *H. helix*). Some naturalized forms not clearly separable from *H. helix*, needs further study. Occurring throughout the San Francisco Bay Area, where capable of being a serious pest plant; probably more common than *H. helix* in that region.

#### Asclepiadaceae

*Asclepias fruticosa* L.: **DIST**: deltaic GV: **CS**: C: **DOC**: **Contra Costa Co.**: Martinez Regional Shoreline, Granger's Wharf Park, north end of Berrelessa St. Aug. 21, 1977, *Walter and Irja Knight* 3158 (CAS): **NOTES**: Narrow leaves like *A. fascicularis*, but pods ovate with long bristles. Not relocated in 2001, but site had been recently denuded by heavy grading.

*Calotropis procera* (Ait.) Ait. f.: **DIST**: DSon: **CS**: C: **DOC**: **Imperial Co.**: agricultural area in the Imperial Valley. August, 1987, *F. Laemmle s.n.* (UCR): **NOTES**: A

solitary shrub, grower was concerned about its potential as a weed and is reported to have destroyed it after sending material for determination.

*Cynanchum louiseae* Kartesz & Gandhi: **DIST**: SCo: **CS**: EXT: **DOC**: **Riverside Co.**: Sanders, A.C. (1996, pg. 526, 527); **NOTES**: The site of this population, which had been established for many years, was re-landscaped recently and the plants could not be relocated in 2001.

#### Asteraceae

*Achillea filipendulina* Lam.: **DIST**: NCo, SCo: **CS**: NCI: **DOC**: **Humboldt Co.**: dense growth in unkempt yard, McKinleyville. July 7, 1975, *F. Bapeaux s.n.* (CDA); **Ventura Co.**: light infestation, 0.01 acre net over 1.0 acre gross, vacant lot, Poncho Rd., Camarillo. T01N, R20W, Sec. 05, SB. June 20, 1979, *H. Carpenter s.n.* (CDA): **NOTES**: Gen. persistent and spreading vegetatively from cultivation, probably rarely reproducing by seed.

*Artemisia vulgaris* L. *sensu stricto*: **DIST**: SCo, SNE: **CS**: NCI: **DOC**: **Ventura Co.**: Waste area of old habitation site between Ventura Ave. and Southern Pacific RR hear Wadstrom. Oct. 10, 1969, *H.M. Pollard s.n.* (CAS, CDA, SBBG); **Mono Co.**: Rock Creek Basin Rd. 0.1 mile N of Mono/Inyo Co. line, just S of Pine Grove Campground, Inyo National Forest. T05S, R30E, Sec. 31, MD. Aug. 12, 1981, *G.D. Barbe* 3532 (CDA): **NOTES**: Determinations by S. Mosyakin (KW), 3/2001. Acc. to Mosyakin, several other non-native taxa of the *A. vulgaris* alliance are represented at CDA but none can at present be associated with a specific name.

*Aster novae-angliae* L.: **DIST**: KR: **CS**: NCI: **DOC**: **Siskiyou Co.**: Single plant in roadside ditch, escape from garden across the rd, Etna, Scotts Valley. Oct. 6, 1966. *T.C. Fuller* 15244 (CDA).

*Carthamus oxyacantha* M. Bieb.: **DIST**: CCo: **CS**: C: **DOC**: **Monterey Co.**: Waif, screening disposal area, vacant field south of spice processing plant, Schilling Place, Salinas. T15S, R03E, Sec. 03, MD. Aug. 2, 1978. *G.D. Barbe* 2421 (CDA): **NOTES**: *Carthamus oxyacantha* is on the Federal Noxious Weed Act quarantine list (see Federal Register, May 25, 2000, p. 33741–33743). Native to South Africa. Related species are aggressive invaders of pastures in New Zealand, Australia, California.

*Centaurea babylonica* L.: **DIST**: n SNH: **CS**: C: **DOC**: **Plumas Co.**: Spontaneous at edge of lawn, to 6 ft tall, large rosette. County Hospital, Quincy. Aug. 7, 1972. *F.H. Surber s.n.* (CDA).

*Chrysanthemum balsamita* L.: **DIST**: CaR: **CS**: C: **DOC**: **Siskiyou Co.**: volunteer, street side, Hennessy St., McCloud. Sept. 17, 1976, *F.D. Horn s.n.* (CDA).

*Cirsium scabrum* (Poir.) Bonnett & Barratte: **DIST**: CCo: **CS**: NCI: **DOC**: **Santa Cruz Co.**: Howell, J.T., (1959, p. 27): **NOTES**: Collection made by A. Eastwood in 1900 and filed under the synonym *Cnicus giganteus* (Desf.) Willd. (UC). Acc. to J. Kartesz, this has also been reported as *Cirsium giganteum* (Desf.) Spreng.

*Coreopsis grandiflora* Hogg. ex Sweet: **DIST**: CaR, SnFrB: **CS**: C: **DOC**: **Alameda Co.**: vacant lot, Appian Way, Union City. June 3, 1976, *E. Whitaker s.n.* (CDA); **Plumas Co.**: Disturbed roadside along Squirrel Ck, USFS road leading to Argentine Rock. Ca. 1 mi NE of Hwy 70, and ca. 7 mi E of Quincy. Elev. 1360 m. 39°55'N; 120°47'30"W. Aug. 22, 1996, *G.F. Hrusa* 13532 (CDA); **San Bernardino Co.**: a single waif, distinct from dwellings, San Bernardino Valley. June 10, 1909, *S.B. Parish* 7131 (UC).

**Cotula mexicana** (DC.) **Cabrera**: **DIST**: CCo, ScV, SnFrB: **CS**: N: **DOC**: **Alameda Co.**: golf course green, Livermore. Apr. 20, 2000, *E. de Villa s.n.* (CDA); golf course green, Hayward. Apr. 26, 2000, *G. Ingram s.n.* (CDA); golf course green, Castro Valley. Apr. 26, 2000, *G. Ingram s.n.* (CDA); **Marin Co.**: golf course green, Novato. Apr. 29, 2000, *G. Ingram s.n.* (CDA); **Monterey Co.**: golf course green, Fort Ord. Nov. 12, 2001, *S. Fennimore s.n.* (CDA, DAV); **Sacramento Co.**: golf course green, Elverta. Dec. 23, 1999, *R. Chavez s.n.* (CDA); golf course green, Sacramento. Jan. 21, 2000, *V. Nyvall s.n.* (CDA); golf course green, Sacramento. Jan. 9, 2000, *F. Carl s.n.* (CDA); golf course green, Galt. Feb. 9, 2000, *D. Thompson s.n.* (CDA); golf course green, Elk Grove. March 16, 2000, *F. Carl, V. Nyvall s.n.* (CDA); **San Mateo Co.**: golf course green, Pacifica. Mar. 21, 2002, *D. Pendleton s.n.* (CDA); *Loc. cit.*, Apr. 18, 2002, (UCR); **Siskiyou Co.**: golf course green, Mt. Shasta region. Dec. 1, 2000, *D. Smith s.n.* (CDA): **NOTES**: A large infestation observed also in **Napa Co.** on a golf course near Pope Valley. Rapidly spreading perennial capable of competing and establishing by seed in mature low cut turf of greens and the adjacent collar. Not yet seen in taller mowed turf, or in wild situations, but expected in the latter. Easily overlooked due to diminutive stature. Native southern Mexico to Bolivia, apparently at elevations above 3000 m.

**Crepis tectorum** L.: **DIST**: SnBr, s SNH: **CS**: N: **DOC**: **Inyo Co.**: Mammoth Lakes, 37°38.8'N, 118°58.5'W, elev. 8100 ft. Uncommon in one local area on roadside among pines. Sept. 26, 1996, *G. Helmkamp 1218* (UCR); **San Bernardino Co.**: Sanders, A.C. (1997b, pg. 307).

**Dendranthema × grandiflorum** Kitam.: **DIST**: SCo: **CS**: NCI: **DOC**: **Ventura Co.**: heavy infestation in yard, Santa Paula. October 27, 1964, *C.J. Barrett and V. Holmer s.n.* (CDA): **NOTES**: This is the florist's chrysanthemum. Original determination as *Chrysanthemum morifolium* Ramat.

**Dittrichia graveolens** (L.) **Greuter**: **DIST**: CCo, SCo, ScV, SnFrB: **CS**: NW: **DOC**: **Alameda Co.**: San Francisco Bay Wildlife Refuge at end of Cushing Road, forming dense masses on levee. Nov. 3, 1995, *B. Ertter 14542* (UC); Shadow Cliffs Recreation Area, Livermore Valley, abundant in riparian woodland. Sept. 28, 1998, *B. Ertter 16412* (UC); Merritt College, common in parking lot on west side of campus. Oct. 8, 2000, *Erter 17540* (UC); Gravelly sidewalk strip at corner of Monaco and Mission Drs. in Pleasanton. 37°39'08"N, 121°52'45"W. Nov. 22, 2000, *D. Petersen 00-54*. (CDA); Niles Cyn. Rd betw. Sunol and Fremont, mile marker 16. In Alameda Cr., sand/gravel bar. 37°35'43"N, 121°54'22"W. Oct. 27, 2001, *D. Petersen s.n.* (CDA); Site M.5 storage area in Camp Parks, Dublin. Disturbed, graveled parking area. 37°43'28"N, 121°52'30"W. Oct. 17, 2001, *D. Petersen 240* (CDA); Arroyo de la Laguna at Verona Bridge (Pleasanton) on gravel bar beside stream. 37°37'35"N, 121°52'55"W. Nov. 14, 2001, *D. Petersen s.n.* (CDA); **Alameda/Contra Costa Co.** [line]: Redwood Regional Park, West Ridge Road. Oct. 15, 2000, *Erter 17541* (UC); **Contra Costa Co.**: Lime Ridge, sterile flat in bowl of quarry area just south of Ygnacio Valley Road, in vicinity of Ygnacio Reservoir, Concord. Locally common. T01N, R01W, Sec. 08, MD. Oct. 18, 1998, *B. Ertter and W.A. Morosco 16423* (JEPS); *loc. cit.* Dec. 29, 1999, *Case and Erter s.n.* (CDA); **San Mateo Co.**: About twenty plants on trailside, E end of Weeks St. adj. to Bay Lands Nature Preserve, E. Palo Alto. Oct. 18, 2001, *J. Beall s.n.* (CDA); **Santa Clara Co.**: Preston, R.E. (1997, 200–203); abundant, two miles north of Alviso Railroad tracks at upper edge of tidal

marsh. Nov. 1, 1984, *H.T. Harvey s.n.* (CDA, SJSU, UC). Det. by C.W. Sharsmith, 5-88.; Overflow channel east of Coyote Creek, 25 yards W of Milpitas Sewage Treatment Plant. ¼ acre. Oct. 16, 2000, *J. Beall s.n.* (CDA, UCR); roadside and in pasture at 4010 Calaveras Rd., Milpitas. Nov. 15, 2000, *N. Garrison s.n.* (CDA); **Solano Co.**: Suisun City, parking lot opposite wildlife center at Peytonia Slough, also near Civic Marina. Oct. 2, 2000, *A.M. Shapiro s.n.* (DAV); **Yolo Co.**: City of West Sacramento, about 0.5 km W of Harbor Blvd., N of West Capitol Ave., along a jeep trail on the S side of the railroad embankment. Oct. 29, 1999, *A.M. Shapiro s.n.* (DAV): **NOTES**: Also noted by Erter at Coyote Hills Recreation Area, and Lake Del Valle; by K. Hintsa at Rock City, Mount Diablo, all **Alameda Co.** D. Petersen (pers. comm. to Hrusa, 10-2001), reports it is becoming common at Camp Parks, **Alameda Co.**, where it occupies creekbanks as well as roadcuts and roadsides. A much-branched, densely glandular, odoriferous, fall-blooming annual, superficially reminiscent of a tarweed but with narrow overlapping phyllaries, or of *Conyza* but with yellow flowers. Ray flowers are reduced, and leaves are alternate. A rapidly spreading invasive weed. R. Preston (personal communication to B. Erter, 1-2000) reports it is now moving into the Central Valley as scattered individuals on most major highways leading inland from the San Francisco Bay Area.

**Emilia fosbergii** D.H. **Nicolson**: **DIST**: SCo: **CS**: GH/C: **DOC**: **San Diego Co.**: Weed in container grown nursery stock. Pleasant Knoll Rd., Valley Center. Feb. 14, 2000, *P. Nolan s.n.* (CDA): **NOTES**: Has also been found as a rare nursery weed in **Sacramento Co.** (ScV) probably in imported soil. Potential garden weed.

**Emilia sonchifolia** (L.) **DC. ex Wight**: **DIST**: SnJV: **CS**: GH/C: **DOC**: **Tulare Co.**: adventive under greenhouse bench; Terra Bella. T23S, R27E, Sec. 12, MD. May 28, 1987, *R.D. Harris s.n.* (CDA): **NOTES**: Potential garden weed.

**Grindelia papposa** Nesom & **Suh**: **DIST**: SCo: **CS**: NCI: **DOC**: **Ventura Co.**: along RR in Ventura. 1962, *H.M. Pollard s.n.* (CAS, SBBG): **NOTES**: Reported in Smith, C.F., (1976, pg. 291) as *Haplopappus ciliatus* (Nutt.) DC., but excluded from the 2nd ed. (Smith, C.F., 1998) and perhaps not persisting.

**Helianthus tuberosus** L.: **DIST**: CCo: **CS**: C: **DOC**: **Alameda/Contra Costa Cos.**: single individuals on both north and south banks of Cerrito Creek near end of Yosemite Avenue at foot of Albany Hill. Sept. 30, 1995, *B. Erter 14526* (UC): **NOTES**: Source is presumably an upstream creekside planting.

**Helichrysum petiolare** Hilliard & **B. L. Burt.**: **DIST**: CCo: **CS**: NW: **DOC**: **Marin Co.**: Matt Davis Trail above Stinson Beach, S side of Mt. Tamalpais, shade of forest, locally common in patches. July 25, 1992, *B. Erter and L. Fujii 11260* (JEPS); 200 m N of Panoramic Hwy, E of Stinson Beach, 200 m from the SW border of Mt. Tamalpais State Park, growing near the remains of an old homestead, nr a larger population of plants 1 km distant. July 2, 1997, *J. Randall s.n.* (DAV); **Monterey Co.**: Open, sunny, sandy soil. Del Monte Forest on the edge of the 1959 burn, Monterey Peninsula. Growing through and up above manzanitas and other shrubs. Jan. 3, 1970, *B. F. Howitt 3117* (CAS, CDA).

**Helioneris multiflora** Nutt. var. **multiflora**: **DIST**: SNE: **CS**: TEN: **DOC**: **Mono Co.**: Mammoth, vacant lot near the Post Office. Aug. 2, 1998, *D.W. Taylor 16936* (UC). Determined by John Strother: **NOTES**: Apparently escaping from nearby areas seeded for 'wildflowers'. The

plants reseed in unmanaged, ruderal vegetation in the developed portion of town, and in this setting reseed as annuals. *Heliomeris multiflora* var. *nevadensis* (Nelson) Yates, a native perennial, occurs in the White Mountains to the east. Brought to our attention by D.W. Taylor.

***Helipterum roseum* (Hook.) Benth.: DIST:** SnFrB: **CS:** NCI: **DOC:** **San Mateo Co.:** McClintock, E., et al. (1990, pg. 79).

***Lasioppermum bipinnatum* (Thunb.) Druce: DIST:** **SCo:** **CS:** NW: **DOC:** **Santa Barbara Co.:** Ross, T. and S. Boyd (1996, 433–434).

***Leontodon muelleri* (Schultz-Bip.) Fiori: DIST:** ScV: **CS:** NCI: **DOC:** **Glenn Co.:** in alfalfa field, 6th and Wyoming Aves, NE of Orland. T22N, R02W, Sec. 08, MD. May 2, 1982, *G. Stenlund s.n.* (CDA).

***Oncosiphon piluliferum* (L.f.) Kallersjo: DIST:** **SCo:** **CS:** N: **DOC:** **Riverside Co.:** Sanders, A.C. (1996, pg. 528); Moreno Valley, E of Lake Perris along JFK Blvd. in disked field. March 23, 1998, *R. Noll s.n.* (OBI, SD). Det. by D. Keil, 11-2001; San Jacinto Wildlife Area, at headquarters off Davis Rd., north of Lakeview. Lakeview 7.5' quad. 33°52'N, 117°07'W; T03S, R02W Sec. 32, SB). Elev. 442 m/1450 ft. July 15, 2001, *O.F. Clarke s.n.* (UCR); San Jacinto Wildlife Area, Lovell Unit approximately 885 m east of Davis Rd and 76 m north of the San Jacinto River levee. Lakeview 7.5' quad, T04S, R02W, Sec. 05, SB. El. 433 m. Alkali playa with *Rumex*, *Crypsis schoenoides*, *Phalaris minor*, *Atriplex argentea*, etc. Traver loamy fine sand, saline alkali. June 18, 1995, *D. Bramlet 2434* (UCR); San Jacinto Wildlife Area, approximately 920 m NW of Lakeview and 487 m west of the Davis Rd, 46 m N of Marvin Rd. Perris 7.5' quad. T04S, R02W, Sec. 06, SB. Elev. 433 m. Alkali playa with *Plagiobothrys leptocladus*, *Crypsis schoenoides*, *Cressa truxillensis*, etc. Willows silty clay. May 6, 1992, *D. Bramlet 2265* (UCR); Romoland, on ramp to Hwy 215 from Hwy 74, just east of Hwy 215. Perris 7.5' quad. 33°45'08"N, 117°11'06"W. Elev. 434 m/1425 ft. Uncommon on disturbed roadside, common in abandoned factory yard across 74 to the south. Also scattered along Hwy 215 all the way to Riverside. May 7, 2001, *A.C. Sanders 24176*, with Mitch Provance and T.B. Salvato (UCR); Val Verde, between Moreno Valley and Perris, along Hwy 215, 0.9 mi S of Oleander Ave., at S end of Patterson Ave. Steele Peak 7.5' quad. 33°50'47"N, 117°15'05"W, T04S, R04W, Sec. 01, SB. El. 457 m/1500 ft. Weedy roadside on disturbed agricultural plains. Locally common on side of freeway, conspicuous for ca. 100 m. May 8, 2001, *A.C. Sanders 24209*, with Mitch Provance and T.B. Salvato (UCR); Moreno Valley, along I-215 just south of the March Field Museum, 0.7 mi S of Van Buren Blvd. Riverside East 7.5' quad. 33°52'35"N, 117°15'52"W; T03S, R04W, Sec. 26, SB. El. 465 m/1525 ft. Weedy roadside on disturbed plains. Locally common and conspicuous for ca. 1 km. May 8, 2001, *A.C. Sanders 24210*, with Mitch Provance and T.B. Salvato (UCR); Lakeview Mtns., Pulsar View Rd, ca. 1 air-mile NE of Juniper Flats Rd. and ca. ¾–1 mi by road from the base of the hills. Lakeview 7.5' quad, 33°49'06"N, 117°05'W; T04S, R02W, Sec. 15, SB. Elev. 610 m/2000 ft. Chaparral, burned within the past few years. Many native wildflowers and some non-natives, all on NW-facing slope. Solitary ind. growing in open spot on the burn. Apr. 11, 1997, *B. Pitzer 3121* (UCR): **San Diego Co.:** San Diego Wild Animal Park, off Hwy 78, E of Escondido in San Pasqual Valley. 33°06'N, 116°59'W. Elev. 300 m/984 ft. Weedy area near back entrance to park. Few plants this year, previously common. Apr. 1998, *Robert Noll s.n.* (UCR); San Diego Wild Animal Park, along back road

behind exhibits (N of African Plains area); also seen on E edge of park and in S African section of Park Botanical Garden. 33°06'N, 116°59'W. Scattered to fairly common at edges of park; abundant among Aloes in S African sect. of Bot. Gdn. Elev. 300 m/984 ft. Mar 25, 1997, *Jan Beyers s.n.* (UCR): **NOTES:** Original report by Sanders was as the synonym *Matricaria globifera* (Thunb.) Fenzl in Harv. and Sond. Comment on the label of the Noll specimen above; "reported also from **Orange Co.**, Haul Cyn. Rd., Irvine Ranch." The current status of this population is not known.

***Osteospermum fruticosum* (L.) Norl.: DIST:** **SCo:** **CS:** NW: **DOC:** **Los Angeles Co.:** Zuma Beach area, mouth of Zuma Creek, E end of the County Beach. major vegetation/habitats are small *Salix lasiolepis* stand w/understory of escaped ornamentals; *Typha/Scirpus* marsh; remnant coastal dunes; disturbed roadsides, former parking area, and rubble dumping area. Site proposed for habitat enhancement. Occasional nr. stream. Point Dume 7.5' quad. 34°01'N, 118°49'W. Elev. <25 ft. Mar. 12, 1997, *S.D. White 4738* (UCR); **Riverside Co.:** Mockingbird Cyn. area, south of Van Buren Blvd. and ca. ½ air mi E of Mockingbird Cyn. Rd Riverside West 7.5' quad. T03S, R05W, Sec. 27, SB; 33°52'N, 117°23'W. Willow riparian with disturbed coastal sage scrub adjacent. May 8, 1989, *Ed LaRue s.n.* (UCR); NW Palomar Mountains, Agua Tibia Mountains; NW foothills of Dorland Mtn.; S end of Los Caballos Road, UC Emerson Oaks Reserve, at the Emerson Cottage. T08S, R02W, Sec. 24, SB. Elev. 1720 ft. Localized escape in *Carpobrotus* plantings from cultivated plants around the Emerson Cabin. May 2, 1996, *Darin L. Banks 0953*, with E.H. Banks (UCR); **San Luis Obispo Co.:** Toro Canyon Rd., E of U.S. Hwy 101, just north of Cayucos. Disturbed soil in farmland. El. 400 ft. Aug. 6, 1989, *G. Helmkmam s.n.* (UCR); **Santa Barbara Co.:** Ferren, W. R., Jr. (1985, pg. 236): **NOTES:** The "freeway daisy" of commerce. Similar to *O. ecklonis*, but growth spreading rather than upright.

***Pericallis cruenta* (DC. non Roth) Webb. & Berth.: DIST:** **CCo:** **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 149); Thomas, H. (1961, p. 374); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 83): **NOTES:** Cited reports are as *Senecio cruentus* DC. non Roth.

***Porophyllum ruderale* (Jacq.) Cass.: DIST:** **SCo:** **CS:** **C:** **DOC:** **Orange Co.:** Weedy areas along roads surrounding vegetable crop field adjacent to Seal Beach Naval Weapons Station. Oct. 17, 2000. *P. Guerrero s.n.* (CDA): **NOTES:** First report for California of this widespread weedy plant, but probably casual as an escape from cultivation. Native (apparently) from Arizona, New Mexico, Texas to South America. Our material referable to the var. *macrocephalum* (DC.) Cronq. (*P. macrocephalum* DC.). Apparently used medicinally and perhaps cultivated in southern California for that purpose.

***Ratibida columnifera* (Nutt.) Wooton & Standl.: DIST:** **CaRH, SCOR:** **CS:** NCI: **DOC:** **Lassen Co.:** Growing in dry, rocky soil on the west side of Eagle Lake, two miles N of the Eagle Lake Resort on service road 33N01. July 21, 1969, *N. Santamaria 721* (CDA, CHSC); In re-growth vegetation in a cleared area at the north end of the Glenn-Eagle airstrip, southwest corner of Eagle Lake, 0.8 mi north of Eagle Lake Resort. T31N, R10E, Sec. 04, MD. Aug. 20, 1974, *G.D. Barbe 1939* (CDA, DAV); **Riverside Co.:** Murrieta, Warm Springs Creek, ca. ½ mile south of Murrieta Hot Springs. 33°35'N, 117°08'W, T07S R03W, SB. Elev. 1500 ft. June 8, 1995, *G.R. Ballmer and K.T. Stockwell s.n.* (UCR), det. by A.C. Sanders,

2002.; June 5, 1996, *K.T. Stockwell s.n.* (UCR); Jurupa Mountains: Glen Avon Heights, on the N side of Conning St. between Campbell and Lindsay Sts. Fontana 7.5' quad. T02S, R06W, Sec. 03, SB. 34°01'35"N, 117°29'45"W, Elev. 860 ft Sandy alluvial slopes. Organic crust which was observed at this location two years ago is no longer present. Solitary perennial. July 30, 2000, *M. Provanca 2173* (UCR); **San Benito Co.**: San Benito. July, 1925, *Mrs. J.A. Bettys s.n.* (JEPS).

***Senecio squalidus* L.: DIST:** SnFrB: **CS:** NCI: **DOC:** **Alameda Co.:** volunteer plants abundant in an uncultivated corner of the experimental growing grounds, U.C. Botanic Garden, Strawberry Canyon, Berkeley. Aug. 20, 1971, *T.C. Fuller 19927* (CDA, DAV); north of corporation/greenhouse area, UC Botanic Garden, Strawberry Canyon, Berkeley. May 17, 1979, *G.D. Barbe 2511* (CDA).

***Tragopogon hybridus* L.: DIST:** CCo: **CS:** NCI: **DOC:** **Monterey Co.:** few plants as waifs, vacant field, Schilling Company, Salinas. T15S, R03E, Sec. 3, MD. May 31, 1978, *J. Lyons and B. Oliver s.n.* (CDA).

***Tripleurospermum maritimum* (L.) W. D. J. Koch: DIST:** NCo: **CS:** TEN: **DOC:** **Mendocino County:** Manchester, at the west end of town on gravel road to the beach, near north edge of Lagoon Creek T13N R17W, Sec 25, MD. Pt. Arena 7.5' quad. El. 80 ft, 39°58'02"N; 123°42'08"W. Dominating a storage area for dairy silage. June 30, 2000, *D. W. Taylor 17473* (JEPS): **NOTES:** =*Matricaria maritima* L. Brought to our attention by D.W. Taylor, det. by J. Strother (UC).

#### Balsaminaceae

***Impatiens balfouri* J.D. Hook.: DIST:** n CCo, NCo, ne SCo, SnFrB: **CS:** N: **DOC:** Wilken, D. (1993, pg. 2): **NOTES:** Included in supplement to Munz but accidentally deleted from Jepson Manual manuscript.

***Impatiens noli-tangere* L.: DIST:** n NCo, SnFrB: **CS:** N: **DOC:** Wilken, D. (1993, pg. 2) also: **Alameda Co.:** Strawberry Creek just above Haas recreation facility behind UC-Berkeley, local colony in moist shade, Aug. 29, 1996, *B. Ertter 15271*, (UC): **NOTES:** Included in supplement to Munz (as *I. occidentalis*) but accidentally deleted from Jepson Manual manuscript.

#### Berberidaceae

***Berberis darwinii* Hook.: DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, pg. 73); Thomas, H. (1961, pg. 172): **NOTES:** Local escape from cultivation.

#### Betulaceae

***Alnus cordata* (Loisel.) Duby: DIST:** NCoRO: **CS:** C: **DOC:** **Sonoma Co.:** Best, C., et al. (1996, pg. 87): **NOTES:** Establishing from landscape planting.

#### Bignoniaceae

***Campsis radicans* (L.) Bureau: DIST:** deltaic GV: **CS:** TEN: **DOC:** **Contra Costa Co.:** Antioch Marina, edge of marsh along roadside. July 11, 1998, *B. Ertter and W.A. Morasco 16370* (UC); **Sacramento Co.:** brushy roadside along Hwy 160 approx. 1 mile S of Freeport and immed. N of Freeport Marina. Twinning in *Vitis californica*, *Rubus discolor*. Not obviously persisting from cultivation. June 9, 2000, *G.F. Hrusa 15440* (CDA, DAV): **NOTES:** A scattered escape from cultivation, possibly marginally naturalized?

***Catalpa bignonioides* Walter: DIST:** n SNF SCo, ScV, SnJV: **CS:** NW: **DOC:** **Amador Co.:** Forster Ranch, along Dry Creek, just east of the Sacramento and San Joaquin Co. lines, 38°19'N; 121°00'W, elev. 50 ft, naturalized. June 6, 1990, *L. LaPré s.n.* (UCR), det. by A.C. Sanders; **Fresno Co.:** Kings River area, east of Centerville, just S of State Hwy 180 (Kings Cyn Rd.), along river, riparian forest and adjacent annual grassland, solitary tree ca. 4 m tall at forest margin near road, perhaps a persisting ornamental planting, though there is no sign of a historic building, 36°43'30"N; 119°28'00"W, T14S, R23E, Sec. 09, MD, elev. 350–400 ft. Apr. 3, 1997, *S. White 4871* (UCR), det. by A.C. Sanders; **Kern Co.:** Bakersfield, E side of the canal at E end of Hart Memorial Park, in a dense thicket of willows, obviously spontaneous. April 25, 1959, *E. Twisselman 5085* (DAV); **Ventura Co.:** Spontaneous in ditch on SPRR ROW at Loma Dr. crossing, Ojai Valley. May 29, 1971, *H.M. Pollard s.n.* (CAS, CDA): **NOTES:** Plants of uncertain status (probably persisting from cultivation) are occasionally found in moist areas in western **Riverside Co.** (e.g., French Valley S of Winchester and San Jacinto River above Cranston Guard Station): Plants of uncertain status observed by Hrusa in **Sacramento Co.** along the American River at American River Parkway and in **Yolo Co.** along Sacramento River 8 mi S of Woodland. Expected elsewhere in low elevation riparian habitats.

#### Boraginaceae

***Echium lusitanicum* L.: DIST:** CCo, NCo: **CS:** TEN: **DOC:** **Monterey Co.:** Rt 68, 1.5 miles south of Pacific Grove, occasional on roadside, May 22, 2000, *G. Leppig 1380* (CDA, HSC); **San Mateo Co.:** common on Rt. 101 roadside and coastal scrub between Montara and Linda Mar. May 24, 2000, *G. Leppig 1384* (CDA, HSC): **NOTES:** Also observed by Leppig as occasional on Rte. 1 in **Mendocino Co.** and on banks of the Gualala River in Gualala (**Sonoma Co.**).

***Pentaglottis sempervirens* (L.) Tausch ex Bailey: DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 118); Thomas, H. (1961, p. 288): **NOTES:** Reported as *Anchusa sempervirens* L.

#### Brassicaceae

***Brassica fruticulosa* Cyrillo: DIST:** SCo, SnFrB: **CS:** N: **DOC:** **Los Angeles, Riverside, San Bernardino Cos.:** Sanders, A.C. (1996, pp. 523–524); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 90).

***Cardamine flexuosa* With.: DIST:** CCo, SCo: **CS:** N: **DOC:** **San Diego Co.:** Vincent, M.A. (1997, pp. 305–306); **San Francisco Co.:** In plantings nr. Fisherman's Wharf. April 8, 1998, *M.A. Vincent and E.H. Fried 8186* (DAV): **NOTES:** Most common as a greenhouse/nursery weed.

***Coincya monensis* (L.) Greuter & Burdet: DIST:** NCo: **CS:** NW: **DOC:** **Humboldt Co.:** Lot ESE of Manila Community Services District sewage pump station; dune sand mixed with gravel fill. Disturbed empty lot with *Senecio vulgaris*, *Lupinus arboreus*, *Holcus lanatus*, *Raphanus sativus*, *Eriogonum latifolium*. Elev. 20'. 40°51'N; 124°10'W. Feb. 13, 1997, *J. Belsher 2* (CDA, DAV, HSC): **NOTES:** Under eradication. Confirmed still present in 1999 (A. Pickart, personal communication).

***Iberis umbellata* L.: DIST:** CCo: **CS:** C: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, pg. 77). Thomas, H. (1961, pg. 185).

***Rorippa sylvestris* (L.) Besser: DIST:** SCo, SnJV: **CS:** TEN: **DOC:** **San Diego Co.:** Nursery property, Sidonia

Rd., Encinitas Ca. Present for several years in this site. May 22, 1998, *C. Elmore s.n.* (CDA, DAV); loc. cit. June 28, 1998, *J. Blasius s.n.* (CDA): **NOTES:** All known sites under eradication. Also confirmed from commercial nursery properties in **San Joaquin Co.** (Lodi), June, 1998; **Ventura Co.** (Oxnard), Jan., 2000. but submitted material not adequate for vouchers. Reproduction by root sprouts only but plants highly persistent; introduced and spread via contaminated nursery stock.

#### Cabombaceae

**Cabomba caroliniana A. Gray:** **DIST:** SnJV: **CS:** NW: **DOC:** **Contra Costa Co.:** Screen trap at Clifton Court Forebay, head of California Water Project. T01S, R04E, Sec. 35, MD. Oct. 18, 2000, *R. Gage s.n.* (CDA); **San Joaquin Co.:** Disappointment Slough NW of Stockton, T02N, R05E, Sec. 09, MD. Sept. 28, 1988; *Griffin et al. s.n.* (CDA); loc. cit. Oct. 6, 1995, *Griffin, Finley s.n.* (CDA); S edge 14 Mile Slough, abundant, with *Egeria densa*, *Myriophyllum spicatum*. T02N, R05E, Sec. 23, MD. Sept. 19, 1991, *E. Finley, R. Villareal s.n.* (CDA); Middle River about Bullfrog Marina. July 24, 2001, *F. Maly s.n.* (CDA): **NOTES:** Reported as common in Lewiston Lake, **Trinity Co.** (DiTomaso personal communication), but no confirming specimen or other plant material has been seen. Recognized by its submerged, deeply divided fan-shaped foliage leaves on distinct petioles. Emerged leaf-like bracts subtending inflorescences at the water surface are oval-perfoliate. Can fill at least a 3 meter water column. A purple-foliaged form is known and although not yet reported for California it is sold in the aquarium trade and is expected. Present in Disappointment Slough since at least 1980 [L. Anderson (USDA) personal communication]. Apparently spreading rapidly in the Sacramento Delta and ultimately to be expected widely. Visual reports need verification as this species has been confused on cursory observation with *Ranunculus aquatilis* from which it differs in its perennial habit and petiolate fan-shaped leaves.

#### Campanulaceae

**Campanula medium L.:** **DIST:** SnBR: **CS:** C: **DOC:** **San Bernardino Co.:** San Bernardino Mtns, N side of Baldwin Lake, at Big Bear Landfill. Former pinyon-juniper woodland, now disturbed and cleared; vegetation weedy except at lower edge, where it is *Chrysothamnus nauseosus* scrub. Solitary plant. Big Bear City 7.5' quad., 34°18'40"N; 116°49'00"W; T03N, R02E, Sec. 30 and Sec. 31, SB. July 3, 2000, *J. Wear s.n.* (UCR), det. by A.C. Sanders.

**Lobelia erinus L.:** **DIST:** SCo: **CS:** C: **DOC:** **Marin Co.:** Howell, J.T. (1970, p. 357); **Santa Barbara Co.:** Escape from cultivation on Cold Spring Road south of and near La Paz Road intersection, Montecito. June 16, 1965, *H.M. Pollard s.n.* (CDA, RSA, SBBG).

#### Caprifoliaceae

**Leycesteria formosa Wallich.:** **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 130–131); Thomas, H. (1961, p. 327): **NOTES:** Reported as a local escape from cultivation.

**Viburnum tinus L.:** **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 131); Thomas, H. (1961, p. 327): **NOTES:** Local escape from cultivation.

#### Caryophyllaceae

**Silene pseudocion Desf.:** **DIST:** CCo: **CS:** NCI: **DOC:** **Monterey Co.:** Howitt, B.F. and J.T. Howell, (1973, pg. 14); road shoulder, old road of Hwy 1, Marina, Calif. March 13, 1970, *A. Allison s.n.* (CAS, CDA), det. by J.T. Howell, 6–4–1970. **San Mateo Co.:** Pacifica property, Redwood City. Mar. 9, 1961, *A. Jillson s.n.* (CDA), det. by N. van Kleeck, 3–1971; **San Francisco Co.:** Single plant, obviously spontaneous, in neglected weedy garden, San Francisco. April 19, 1972, *J.T. Howell 48673* (CAS, CDA, DAV).

#### Celastraceae

**Maytenus boaria Molina:** **DIST:** SnFrB: **CS:** NW: **DOC:** **Alameda Co.:** Gwinn Canyon in Oakland Hills, north side of Marlborough Drive, regrowth of scrub after major fire. June 21, 1994, *B. Ertter 12838a* (UC); loc. cit. Aug. 29, 1997, *E. Leong s.n.* (UC): **NOTES:** A well-known ornamental small tree with drooping branches, narrowly rhombic, toothed leaves, and inconspicuous flowers. Considered a pest plant locally, with control efforts underway. Germinates profusely following fire.

#### Chenopodiaceae

**Atriplex muelleri Benth.:** **DIST:** DSon: **CS:** NCI: **DOC:** **Riverside Co.:** 20 miles west of Blythe, a single plant on roadside. Oct. 17, 1965, *J.C. Roos s.n.* (COLO, UC, UCR): **NOTES:** Perhaps extirpated, sporadic searches over past 10+ years by Sanders have not found this.

**Chenopodium watsonii A. Nels.:** **DIST:** SnGB: **CS:** NCI: **DOC:** **Los Angeles Co.:** Big Tujunga at Colby Ranch Rd. Elev. 3200 ft. Dry sunny sandy roadside. Oct. 1, 1966, *L.C. Wheeler 8941* (CDA, RSA): **NOTES:** Determination by S.E. Clemants (BKL) and S. Mosyakin (KW), 3–2001. Original determination as *C. album* L., distinguished readily by the whitened reticulate seed coat of *C. watsonii*. Native in the Great Basin region, further collections and distribution data are necessary to determine if this is introduced or an overlooked California native.

**Salsola kali L. subsp. pontica (Pallas) Mosyakin:** **DIST:** DMOj, s ChI: **CS:** NCI: **DOC:** **Kern Co.:** Mouth of Red Rock Cyn. Plant yellow-green, growing in shady probably sub-alkaline soil in dry wash. Occasional—common in such places. Elev. 2300 ft. Creosote bush association. Aug. 22, 1961, *E.C. Twisselmann 6468* (DAV). Det. by S. Mosyakin 3–2001. **Ventura Co.:** Mosyakin, S.L. (1996, pg. 389): **NOTES:** Ventura County record is a single collection from San Nicolas Island. U.S. Naval Radiological Defense Laboratory, near road above sand spit at 100 feet elevation, *R. E. Foreman 42* (US). Label data provided by S. Mosyakin (KW).

#### Cistaceae

**Halimium lasianthum (Lam.) Spach:** **DIST:** SCo: **CS:** NCI: **DOC:** **Ventura Co.:** escaped in yards in Oxnard. June, 1949, *V. Holmer s.n.* (CDA): **NOTES:** Det. by M.K. Bellue.

#### Convolvulaceae

**Calystegia silvatica (Kit.) Griseb. subsp. disjuncta Brummitt:** **DIST:** NCo, SnFrB: **CS:** N: **DOC:** **Alameda Co.:** Codornices Creek at southwest corner of Albany Village. May 22, 2000, *M. Hurlbert s.n.* (JEPS): **Humboldt Co.:** Growing in waste area at the intersection of 11th and B Sts, Arcata. Moist gulch. Aug. 10, 1976, *T. Nelson 3166*



(CDA); Arcata, 11th and B. St., empty lot. July 8, 2001, *G. Leppig 1577* (CDA, HSC); Eureka, Waterfront Dr. waste area, 100 m N Humboldt County Library. July 10, 2001, *G. Leppig 1578* (CDA, HSC); Arcata, South G St. adj. to city of Arcata Corporation Yd. Waste area, roadside. July 11, 2001, *G. Leppig 1579* (HSC, UC); **Marin Co.**: Brummitt, R.K. (Madrono, in press); **NOTES**: Previously confused with *C. sepium* subsp. *limnophila* (Greene) Brummitt, but readily distinguished by its larger flowers (5–7.5 cm), inflated bracteoles that hide the calyx, larger leaves, and glabrous vestiture. Sporadic but persistent in urban waste areas around Humboldt Bay.

**Convolvulus tricolor L.**: **DIST**: CCo: **CS**: NCI: **DOC**: **Monterey Co.**: adventive, vacant field adjacent to Schilling Company processing plant, Salinas. T15S, R03E, Sec. 03, MD. April 24, 1979, *J.L. Johnson and B. Oliver s.n.* (CDA), det. by G.D. Barbe, April 1979 at CAS.

**Dichondra micrantha Urb.**: **DIST**: n SNF, SCo, SnFrB: **CS**: NCI: **DOC**: **Butte Co.**: Heavy infestation, 1 acre, 1 mi E of Quincy Rd. and 1 mi S of Middle Fork Feather River on W side of Bidwell Mtn. Private property, June 7, 1963, *W. Hansell s.n.* (CDA), det. by T.C. Fuller; **Los Angeles Co.**: El Segundo Dunes, W of Los Angeles Int. Airport and Pershing Dr. 33°56'N, 118°26'W. Elev. 125 ft. Sept. 18, 1987, *A.C. Sanders 7367* (UCR); **Riverside Co.**: Hemet, SE corner of State St. and Bibbel, 1712 ft hill at east end of Diamond Valley. Hemet 7.5' quad. 33°42'N, 116°58'W; T05S, R01W, Secs. 26, 27, 34, 35, SB, common corner. Elev. 494–518 m/1620–1700 ft. Scarce at margins of dried pool and in disturbed soil. May 3, 2001, *A.C. Sanders 24113* (UCR); **San Bernardino Co.**: San Bernardino Mtns., E of Yucaipa, Water Cyn., trib. of Wildwood Cyn. from the N. Vicinity of old Hunt Ranch, ca. ¾ mi. N of Wildwood Canyon Rd. (T02S R01W Sec. 04, SB. 34°01'30"N, 116°59'30"W) Elev. 3300 ft. Fairly common on roadside at edge of barren cattle corral where clearly naturalized. June 5, 1992, *A.C. Sanders 12365*, with *E.J. Lott and D. Pendleton* (UCR); **Ventura Co.**: Flood plain of Coyote Creek nr. confluence with Ventura River, Foster Park. Oct. 15, 1969, *H.M. Pollard s.n.* (DAV); **NOTES**: Also noted on embankment of Cerrito Cr., spreading beyond lawn of Creekside Park (**Contra Costa Co.**). Expected elsewhere. Cited in Munz (1974, pg. 379) as *Dichondra repens* Forst. & Forst.f. which is misapplied in California to *D. micrantha*, the common cultivated lawn substitute. *Dichondra repens* has also been misapplied in California to the native *Dichondra donnelliana* Tharp & Johnston, thus care must be taken, specifically a specimen observed, when applying an epithet to a reported occurrence identified as *D. repens*. Again, the importance of documenting voucher specimens is clear; in this case the holotype of *Dichondra donnelliana* was originally determined as *D. repens*!

**Ipomoea aquatica Forssk.**: **DIST**: ScV: **CS**: C: **DOC**: **Sutter Co.**: Weed in cultivated, diverse, vegetable row crop. Wet. Mung garden N of Yuba City. Oct. 1, 2001, *G.F. Hrusa 15989* (CDA); **NOTES**: Becoming widely (and illegally) cultivated as a greenhouse crop in California, less commonly as a row crop in the Central Valley, with weedy occurrences thus expected to increase in frequency. A potential aquatic pest in warm areas. Federal Noxious Weed.

**Ipomoea lacunosa L.**: **DIST**: CCo: **CS**: C: **DOC**: **Santa Cruz Co.**: Aptos, watershed of Aptos Creek adjoining Nisene Marks State Park, weed along 3000 block of Redwood Drive; elev. 550 ft, 37°00'45"N; 121°54'00"W. Disturbed opening of residential yard in *Sequoia sempervirens*-*Lithocarpus densiflorus*-*Quercus parvula* var. *shrevei*

dominated forest. Waif from birdseed originating from bird feeder. With waif *Panicum* sp. and *Helianthus annuus*. Sept. 6, 2000, *D.W. Taylor 17585* (JEPS); **NOTES**: Perhaps trivial, but to be expected elsewhere. Originated from 'National Audubon Society Superior Wild Bird Food' [4.53 kg—Wagner Bros. Feed Corp.] purchased ca. spring, 2000. Native to eastern North America. The identity of the *Panicum* sp. is unknown because it does not [has not] flowered.

**Ipomoea quamoclit L.**: **DIST**: GV: **CS**: C: **DOC**: **Sacramento Co.**: volunteer in residential garden, climbing on roses, Sacramento. April 17, 1992, *Joe Bandi s.n.* (CDA).

#### Crassulaceae

**Crassula multicava Lem.**: **DIST**: CCo: **CS**: NW: **DOC**: **Monterey Co.**: Pt. Lobos State Reserve. Rock crevices along the trail at Big Dome Cove, granite rock outcrops in *Pinus radiata* forest, with abundant *Polypodium calirhiza* and lichens, 36°32'01"N; 120°56'50"W. Feb. 2, 1998, *D.W. Taylor 16282* (JEPS, UC), det. by Dean Kelch (UC); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 102); **NOTES**: Reproducing by bulbils. This species was reported for Monterey County by Yadon (1995) but was not included in Matthews, M.A. (1997). Report and data provided by D.W. Taylor.

**Sedum album L.**: **DIST**: c SNF, SnFrB: **CS**: N: **DOC**: **Tuolumne Co.**: Yosemite Valley, Yosemite National Park, ruderal disturbed margin of paths and parking area in employee housing tents on southeast edge of Yosemite Village area, disturbed margin of parking areas and paths in open sunny locations, 3900 ft, 37°44'35"N; 119°34'48"W. Sept. 9, 1997, *D.W. Taylor 16266* (JEPS, UC); **NOTES**: Report and data provided by D.W. Taylor. Also observed spreading beyond cultivation into overflow basin in Creekside Park, El Cerrito (**Contra Costa Co.**).

**Sedum dendroideum Sesse & Moc. ex DC.**: **DIST**: CCo: **CS**: NCI: **DOC**: **San Francisco Co.**: Howell, J.T. et al. (1958, p. 80); Thomas, H. (1961, p. 188); **NOTES**: Local escape from cultivation.

#### Cucurbitaceae

**Cucumis anguria L.**: **DIST**: SnJV: **CS**: NCI: **DOC**: **Madera Co.**: in highway right-of-way, Madera. July 1939, *M. Bellue s.n.* (UC).

**Cucurbita ficifolia Bouche**: **DIST**: SCo: **CS**: NCI: **DOC**: **Ventura Co.**: Adventive on the waste ground of a once inhabited site betw. Ventura Ave. and So. Pac. RR nr. Wadstrom, Ventura Oil Fields. Nov. 27, 1968, *H.M. Pollard s.n.* (CDA).

**Cucurbita pepo L. var. medullosa Alef.**: **DIST**: NCoRO: **CS**: C: **DOC**: **Sonoma Co.**: Best, C., et al. (1996, pg. 118); **NOTES**: The zucchini of commerce escaping locally.

#### Cuscutaceae

**Cuscuta reflexa Roxb.**: **DIST**: SCo: **CS**: EXT: **DOC**: **Los Angeles Co.**: Abundant on *Hedera canariensis*, N side Biology Bldg., Cal State Los Angeles. October 23, 1969, *T.C. Fuller 19021* (CDA); **NOTES**: State listed Noxious Weed. Now eradicated, this was the only known occurrence in North America north of Mexico.

#### Droseraceae

**Drosera aliciae Hamet**: **DIST**: NCoRO: **CS**: NCI: **DOC**: **Mendocino Co.**: Meyers-Rice (Madrono, in press); restricted to its introduction site in a wet depression in a

pygmy forest, 39°15'N; 123°45'W. Nov. 2, 1997, *B. Meyers-Rice MR971101* (DAV); **NOTES:** Intentionally introduced.

***Drosera capensis* L.: DIST:** NCoRO: **CS:** NCI: **DOC:** **Mendocino Co.:** Meyers-Rice (Madrono, in press); several scattered colonies of naturalized plants spreading through wet depressions and seeps in a pygmy forest, 39°15'N; 123°45'W. Nov. 2, 1997, *B. Meyers-Rice MR971103* (DAV); **NOTES:** Intentionally introduced. According to B. Meyers-Rice (DAV) this species is probably *D. linearis* auct. non Goldie, as per Smith, G. and C. Wheeler (1990–1991, pg. 170) and Hickman, J.C. ed. (1993, pg. 541).

***Drosera tracyi* MacFarlane: DIST:** NCoRO: **CS:** NW: **DOC:** **Mendocino Co.:** Smith, G. and C. Wheeler (1990–1991, pg. 170); **NOTES:** Intentionally introduced. Sometimes treated within *D. filiformis* Raf. According to B. Meyers-Rice (DAV) both typical *D. filiformis* (as mentioned in Hickman, ed. 1993) and *D. tracyi* are found at this site.

#### Ebenaceae

***Diospyros virginiana* L. var. *virginiana*: DIST:** SnBr: **CS:** NCI (in Mendocino Co.). NW (as clonal colonies in San Bernardino Co.): **DOC:** **Mendocino Co.:** Hopland Field Station, headquarters nr. office. June 14, 1959, *AHM s.n.* (AHUC); **San Bernardino Co.:** San Bernardino Mtns. Mill Creek Canyon, on S side of Hwy 38, 1.2 mi above Mountain Home Creek at Mountain Home Village, Forest Falls 7.5' quad., 34°06'N; 116°58'30"W, T01S, R01W, Sec. 10, SB. Elev. 4040 ft/1232 m. Dry meadow w/scattered trees on alluvial bench in canyon bottom, sandy loam w/rocks. Single trees of *Pyrus communis* and *Prunus cerasifera* also present. Could be old orchard site, but vegetation looked natural, w/no sign of former occupation; possibly a few spp. escaped from cultivation at Mountain Home. Grove of 74 trees, 2–9 m tall; oldest (75–100 yr) dead but 45 cm dbh, live trees 6–12 cm; corollas pale yellow, mostly w/4 lobes, but occasionally 5. Grove all female?, possibly from sprouts of old tree. Fruits produced; but seeds? Discovered ca. 1983 by Goodman. Bark dark and deeply fissured into blocks, covered w/lichens. June 26, 1999, A.C. Sanders 22903 with *John Goodman* (ARIZ, CAS, MO, RSA, SD, UCR, UNLV, UTEP); loc. cit. Nov. 11, 1999, A.C. Sanders 23252 with *Mihai Costea*, T. B. Salvato (UCR); Near Old Mormon Road Monument on old loop off Hwy 18 below Crestline, San Bernardino North 7.5' quad., T02N, R04W, Sec. 27, SB. 34°13'30"N; 117°17'30"W. Elev. 4200 ft/1280 m, canyon woodland. Scarce tree ca. 20 m tall and 38 cm dbh. Roadside, presumably originally planted (possibly from discarded seed?), but with a number of saplings (10–15) derived from root-sprouts surrounding parent tree. Straight central trunk with small angled branches, square-checked bark. July 21, 2000, A.C. Sanders 23591 with *N. Diep* (UCR); **NOTES:** The Mendocino Co. specimen at AHUC may or may not document a spontaneous occurrence. Otherwise only two known populations but both are reproducing vegetatively and have been present for decades. Plants are vigorous and obviously successful under natural conditions. A population with both sexes present might be even more successful.

#### Elaeocarpaceae

***Aristotelia chilensis* (Molina) Stuntz [A. macqui L'Her.]: DIST:** SnFrB: **CS:** TEN: **DOC:** **Alameda Co.:** Strawberry Creek near Life Sciences complex on UC-

Berkeley Campus, common shrub in understory along creek. May 23, 2000, B. Erter *s.n.* (UC).

***Muntingia calabura* L.: DIST:** SnJV: **CS:** GH/C: **DOC:** **Stanislaus Co.:** Spontaneous in coco fiber imported from Sri Lanka, greenhouse hydroponic operation. Nov. 11, 1997, T. Watson *s.n.* (CDA); **NOTES:** Worldwide weed of the tropics and wet subtropics, indigenous to S. America. In California known only as a greenhouse weed (seedlings). May be expected to volunteer and persist under mild, moist conditions, esp. cultivated sites.

#### Escalloniaceae

***Escallonia macrantha* Hook. & Arn.: DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 81); Thomas, H. (1961, p. 192).

#### Euphorbiaceae

***Euphorbia characias* L.: DIST:** CCo: **CS:** NCI: **DOC:** **Alameda Co.:** Albany waterfront, on former landfill, local colony (probably extirpated by subsequent park development). Aug. 19, 1994, B. Erter 13076 (UC); **NOTES:** Single plant also noted on adjacent Albany Hill. Commonly grown as an ornamental.

***Euphorbia cyathophora* Murr.: DIST:** SCo, SnJV: **CS:** NCI: **DOC:** **Fresno Co.:** to six feet, in roses, etc., Fresno. Oct. 28, 1959, T.C. Fuller 3213 (CDA); **Ventura Co.:** light infestation on roadside fill, Olsen Rd. betw. Thousand Oaks and Simi. Feb. 10, 1971, *Hannah s.n.* (CDA), det. by T.C. Fuller.

***Euphorbia dendroides* L.: DIST:** SCo: **CS:** NW: **DOC:** **Los Angeles Co.:** Sanders, A.C. (1997a, 203); Foothills, San Gabriel Mtns., Eaton Cyn nr. Kinneloa Mesa, Pasadena. T01N, R12W, Sec. 13, SB. Mar. 30, 1981, *S. Granger s.n.* (CDA, RSA); Chantry Flats Ranger St., Big Santa Anita Cyn. Angeles Nat. Forest. May 21, 2002, *J. Hartman, s.n.* (CDA, UC/JEPS, UCR); **Santa Barbara Co.:** Smith, C.F. (1976, pg. 184); Santa Barbara, Franceschi Park, naturalized along rocky slope of Mission Ridge Rd. Sept. 5, 1950, C.F. Smith 2859 (DAV, SBBG); loc. cit. Feb. 13, 1952, C.F. Smith 3224 (DAV, SBBG); Escaped on hillside, S of Franceschi Park, Santa Barbara. May 7, 1959, T.C. Fuller 2433. (CDA, DAV); Vacant field NE of Old Mission Santa Barbara. June 11, 1970, C.F. Smith 10229 (DAV, SBBG); **Ventura Co.:** Few scattered plants, Peto Seed Co. Ranch, Saticoy. May 20, 1959, T.C. Fuller 2435 (CDA); **NOTES:** Several additional collections at DAV from the Franceschi Park locality, all from the 1950s, are not detailed here.

***Euphorbia heterophylla* L.: DIST:** ScV: **CS:** NCI: **DOC:** **Sutter Co.:** Weedy in 4 acre mung bean crop, present for past 2 seasons, 0.15 mi S of Nuestro Rd, W side Terra Buena Rd. NW Yuba City. Sept. 26, 1984, G.D. Barbe 4104 (CDA, DAV); **NOTES:** Reported also as an uncommon weed in the UCR (**Riverside Co.**) Botanic Garden.

***Euphorbia hirta* L.: DIST:** SCo: **CS:** N: **DOC:** **Riverside Co.:** Sanders, A.C. (1997a, 203–4); **NOTES:** Sometimes treated as *Chamaesyce hirta* (L.) Millsp. Has been intercepted as a weed of nursery stock from the southeastern states, esp. Florida.

***Euphorbia hypericifolia* L.: DIST:** CCo, ScV: **CS:** GH/C: **DOC:** **Monterey Co.:** Town of Aromas, Blue Pacific Greenhouses at the corner of Carpenteria Rd. and San Juan Rd. Aug. 21, 2000, *M. Inaba s.n.* (DAV); **Sacramento Co.:** 12676 Stockton Blvd., uncommon ascending weed in greenhouse, presumably imported from Florida or Hawaii with foliage plants. May 23, 1988, *D. Koutnik s.n.*



(DAV): **NOTES:** All original determinations as *Chamaesyce hypericifolia* (L.) Mills.

**Euphorbia marginata Pursh:** **DIST:** KR, n SNF, ScV, SCo: **CS:** NCI: **DOC:** El Dorado Co.: S of Camino on rd to Pleasant Valley, adventive in roadfill. Aug. 7, 1977, G.L. Stebbins 77136 (DAV); **Placer Co.:** Limited light infestation, SPRR yards, Roseville. T10N, R06E, Sec. 11, MD. Aug. 26, 1971, Henderson s.n. (CDA); **Shasta Co.:** Limited heavy infestation, roadside, 100 ft N of Calif. Forestry Station, French Gulch, Clear Ck. Cyn. T33N, R07W, Sec. 02, MD. Elev. 1500'. Sept. 8, 1970, P. Whipp s.n. (CDA); **Ventura Co.:** Spontaneous in waste ground, Junipero St. betw. Santa Clara and Main Sts. Ventura. July 12, 1966, H.M. Pollard s.n. (CAS, CDA); spontaneous on ground cleared for waterfront development. Front and Palm Sts, Ventura. July 11, 20, 28, 1967, H.M. Pollard s.n. (CAS, CDA).

**Euphorbia myrsinites L.:** **DIST:** TR: **CS:** NCI: **DOC:** Kern Co.: Single plant on stream bank, Vine Street, Frazier Park. T09N, R20W, Sec. 35, SB. May 14, 1981, J. Marks s.n. (CDA), det. by T.C. Fuller.

**Euphorbia rigida M. Bieb.:** **DIST:** SnJV, SCo: **CS:** NCI: **DOC:** Tulare Co.: escaped from cultivation, RR ROW SE of Porterville. T22S, R28E, Sec. 06, MD. March, 1993, Ahrendes s.n. (CDA); **Ventura Co.:** 3–4 large plants established in grassy, weedy area, Erbs Rd., Thousand Oaks. March 30, 1967, Schall s.n. (CDA); in ice plant groundcover, median highway strip along US Hwy. 101 ca. 3 mi E of Ventura. Feb. 27, 1976, C. Elmore s.n. (DAV).

**Euphorbia terracina L.:** **DIST:** SCo: **CS:** NW: **DOC:** Los Angeles Co.: Sanders, A.C. (1997a, 205); Volunteer in UCLA Botanic Garden. Oct. 23, 1967, T.C. Fuller 16495 (CDA); El Segundo Dunes, immed. W of LAX. May 18, 1988, A.C. Sanders 7832 (UCR, CDA); Solstice Canyon, Santa Monica National Recreation Area. T01S, R18W, Sec. 16, SB. Mar. 22, 2001, S. Williams s.n. (CDA); Monterey Park. Garvey Reservoir, dry slope above dam. T01S, R12W, Sec. 26, SB. June 26, 2001, J. Hartman and M. Adams s.n. (CDA); Palos Verdes Peninsula, Rancho Palos Verdes, Ocean Trails development, between Palos Verdes Dr. South and the ocean. San Pedro 7.5' quad. 33°43'37"N, 118°20'30"W. Elev. 2–10 ft. Base of coastal bluffs. July 17, 2001, Jeremiah George s.n. (UCR), det. by A.C. Sanders; Zuma Beach area, mouth of Zuma Creek, E end of the County Beach, ca. 100–200 plants on W bank of the stream, in sand, and on adjacent remnant dunes. Point Dume 7.5' quad. 34°01'N, 118°49'W. Elev. <25 ft. Mar. 12, 1997, S.D. White 4750 (UCR), det. A.C. Sanders; Santa Monica Mtns., Malibu Lagoon, Malibu Beach State Park, mouth of Malibu Creek. Malibu Beach 7.5' quad. 34°02'N, 118°41'W; T01S, R17W Sec. 32, SB. Elev. 8 m/25 ft. Fairly common perennial at edges of cultivated areas at Adamson house. Oct. 10, 1998, A.C. Sanders 22259 (UCR); same as previous, but: uncommon at edge of road (Cross Creek) on W side of lagoon. Oct. 10, 1998, A.C. Sanders 22260 (UCR): **NOTES:** Monterey Park form may be at least facultatively annual, warrants further study.

**Sapium sebiferum (L.) Roxb.:** **DIST:** ScV: **CS:** NW: **DOC:** Sacramento Co.: On the N bank of American River in the American River Parkway, few hundred meters downstream of the Estates Drive entrance. 38°33'N; 121°22'W. June 28, 1998, B. Meyers-Rice MR980603 (CDA, DAV): **NOTES:** Ornamental, commonly cultivated in the residential areas surrounding the American River Parkway. Has the potential to naturalize locally in California. Reported from SnFrB, but no confirming speci-

mens have been seen. A serious pest in the summer wet southeastern U.S.

## Fabaceae

**Astragalus cicer L.:** **DIST:** c SNF: **CS:** TEN: **DOC:** Tuolumne Co.: Disturbed waste area nr. Standard. July 4, 1998, M. Chambers s.n. (CDA): **NOTES:** Persisting in this site for several years previous to 1998 and observed in 1999.

**Cassia nemophila A. Cunn.:** **DIST:** DSon: **CS:** TEN: **DOC:** Riverside Co.: Coachella Valley, between La Quinta and Indio, along Jefferson St. between Ave 54 and I-10, 33°41'N; 116°16'W, T06S, R07E, Sec. 04, elev. 10 m. Fairly common 1–2 m shrub, scattered on roadside and in adjacent old fields, cultivated nearby in center divider of Jefferson St. and spreading by seed into adjacent dry lands. May 28, 1999, A.C. Sanders 22794 (UCR, and to be distributed): **NOTES:** Reproducing without care in one of the driest parts of the state. [This belongs in *Senna*, but as of 1986 the appropriate combination had not been published (R. Barneby, personal communication; Royal Hort. Dict. Gardening, 1992, says the same, but uses the *Senna nemophila* combination anyway "awaiting publication")].

**Ceratonia siliqua L.:** **DIST:** SCo: **CS:** NW: **DOC:** Los Angeles, Riverside, San Bernardino Cos.: Sanders, A.C. (1996, pg. 526).

**Coronilla valentina L.:** **DIST:** SCo, s ChI: **CS:** NW: **DOC:** Los Angeles Co.: Ross, T. and S. Boyd (1996, pg. 435).

**Dolichos lignosus Pers.:** **DIST:** SCo: **CS:** NCI: **DOC:** San Diego Co.: Beauchamp, R. M. (1986, pg. 157).

**Genista monosperma (L.) Lam, non Link, nec Del.:** **DIST:** SCo: **CS:** NW: **DOC:** Los Angeles Co.: San Gabriel Mtns, base of range at Padua Hills, W of mouth San Antonio Cyn. Disturbed alluvial fan and adjacent slopes with chaparral. Feb. 3, 1990, S. Boyd 3828 (CDA, RSA): **San Diego Co.:** South of Fallbrook. 100 yds W of Olive Hill Rd, approx. ¼ mi S of Mission Rd. (rd S13), S side of Color Spot nursery. June 19, 2000, J. Giessow s.n. (CDA and to be distributed): **NOTES:** Original det. by E. McClintock (CAS); label det. of Boyd 3828 as *Genista aetnensis* (Biv.) DC. Treated in Flora Europaea as *Lygos monosperma* (L.) Heywood and listed by CalEPPC as *Retama monosperma* (L.) Boiss. We find the generic distinctions dubious. Under eradication on adjacent Camp Pendleton federal lands (personal communication from E. Johnson, May 2000). Specimen cited in Rejmanek and Randall (1994) as at DAV apparently was never deposited.

**Gleditsia triacanthos L.:** **DIST:** GV: **CS:** NW: **DOC:** Sacramento Co.: Randall, J.M. and B. Meyers-Rice (1997, pp. 399–400).

**Lathyrus sativus L.:** **DIST:** CCo, NCoRO: **CS:** C: **DOC:** San Luis Obispo Co.: Spontaneous in garbanzo bean field, opposite Los Osos Valley Memorial Park Cemetery, W end of Los Osos Valley. July 22, 1971, J.H. Foott s.n. (CDA, DAV); **Sonoma Co.:** Best, C., et al. (1996, pg. 131).

**Ononis alopecuroides L.:** **DIST:** SCoRO: **CS:** NW: **DOC:** San Luis Obispo Co.: Hrusa, G.F. (2000, pg. 139): **NOTES:** Known from a single large population, currently under eradication by San Luis Obispo Co. Agricultural Commissioner's Office.

**Robinia hispida L.:** **DIST:** ScV: **CS:** N: **DOC:** Sacramento Co.: Colony on bank of Sacramento River at divergence of Steamboat Slough, SW corner of Steamboat Bridge. Root-sprouting, spreading from planted plants down bank, forming a thicket beneath *Robinia pseudo-*

*acacia*. Apr. 9, 2000, *G.F. Hrusa 15318* (CDA and to be distributed): **NOTES:** Locally naturalized, but apparently spreading only vegetatively. *Robinia hispida* consists of a series of clones, reproducing facultatively by rootsprouts and agamospermic seeds (Isely, 1998). Several forms are cultivated.

*Senna artemisioides* (Gaudich. ex DC.) **Randell:** **DIST:** SnBr, SnGb: **CS:** N: **DOC:** Los Angeles Co.: San Gabriel Mts, north of Claremont, along Burbank Fire Road in Burbank Canyon, west of Palmer Canyon; growing near edge of gravel road, naturalized in area. Jan. 24, 1993, *T.S. Elias 12445* (UC); **San Bernardino Co.:** North of San Bernardino along Hwy 18, 0.2 miles above the lower end of old Waterman Canyon Road, SW side of highway on road fill, growing wild. Mar. 9, 1984, *F.C. Vasek s.n.* (UCR): **NOTES:** Population still extant ca. 1995–1998 in lower Waterman Canyon just above Hwy 18. All specimens labeled as *Cassia artemisioides* Gaudich. ex DC.

*Senna obtusifolia* (L.) **H.S. Irwin & Barneby:** **DIST:** DSon, SnJV: **CS:** N in DSon; TEN in SnJV: **DOC:** Riverside Co.: Sanders, A.C. (1996, pg. 531): **NOTES:** A single individual also found on a roadside in Fresno Co., sent without additional data to CDA for confirmation; material in condition too poor for vouchering.

*Sesbania punicea* (Cav.) **Benth.:** **DIST:** CaRF, GV, NCoRO: **CS:** N: **DOC:** Butte Co.: Shrub on wet sand, margin of small pond, ½ mile W of Pacific Heights Rd., Oroville Wildlife Area. T18N, R03E, Sec. 03, MD, elev. 140 ft. Aug. 23, 2000, *L. Ahart 8660* (CDA, CHSC). **Fresno Co.:** gravel pit ponds, Pinedale. June, 1988, *J. Dunitz s.n.* (CDA); **Sacramento Co.:** On the margins of William Pond in the American River Parkway, Arden Rd. entrance. 38°33'N; 121°22'W. June 28, 1998, *B. Meyers-Rice MR980604* (CDA, DAV); **Shasta Co.:** E side Hwy 273 in Redding, immed. S of Breslauer Rd. Shrubs in wash bet. Hwy and RR tracks. Aug. 21, 2000, *K. Martyn s.n.* (CDA); Riverview Country Club, Bechelli Lane. Extensive lakeshore infestation. Dec. 11, 2001, *K. Martyn s.n.* (CDA); **Sonoma Co.:** Best, C., et al. (1996, pg. 140): **NOTES:** Sonoma County report as *S. tripletii* Host.

*Trifolium alexandrinum* L.: **DIST:** CCo, ScV: **CS:** NCI: **DOC:** Butte Co.: South side of Evans-Reimer Rd., ca. 1 mi E of Pennington Rd., Gray Lodge Waterfowl Management Area. May 10, 2001, *L. Ahart 8738* (CDA, CHSC, UC); **Monterey Co.:** few waifs, vacant field. Schilling Co., Salinas. T15S, R03E, Sec. 03, MD. May 31, 1978, *J. Lyons and B. Oliver s.n.* (CDA).

*Trifolium cernuum* Brot.: **DIST:** ScV: **CS:** N: **DOC:** Butte Co.: Near boat ramp off Larkin Rd., Thermalito Afterbay, Lake Oroville. May 13, 2000, *L. Ahart 8343* (CHSC, MU, UC/JEPS): **NOTES:** Determination confirmed by M. Vincent (MU). Reported in Oswald, V. (2000). Naturalization local.

*Trifolium gemellum* Poir. ex Willd.: **DIST:** CCo, SnFrB: **CS:** N: **DOC:** Napa Co.: Henry Road 1.7 miles northwest of Dealy Lane [SW of city of Napa]. Common on open, grassy, southwest-facing slope in *Quercus agrifolia* woodland, elev. 450 ft, T05N, R05W, Sec 12, MD. May 12, 2000, *J. Ruygt 4248* (UC): **NOTES:** Naturalization local. Report and data provided by J. Ruygt.

*Trifolium resupinatum* L.: **DIST:** NCo, CCo, ScV, SCo: **CS:** NCI: **DOC:** Humboldt Co.: immediate vicinity of Eureka, a single plant. May 14, 1896 and July 8, 1897, *J.P. Tracy 105* (UC); **Monterey Co.:** few scattered plants in vacant field, flowers pinkish; Schilling company, Salinas. T15S, R03E, Sec. 03, MD. May 11, 1978, *J. Bunch and B. Oliver s.n.* (CDA); **Santa Barbara Co.:** Howell,

J.T. (1972, pg. 103); Smith, C.F. (1976, pg. 179); **Sutter Co.:** Edge of field, 3 miles S of Oswald. June 11, 1967, *J.T. Howell 42556 and G.H. True* (CAS, CDA); **Ventura Co.:** Howell, J.T. (1972, pg. 103): **NOTES:** Probably only casual.

*Trifolium retusum* L.: **DIST:** CaRF: **CS:** NW: **DOC:** Tehama Co.: Calif. Dept. of Fish and Game parcel on west side of Manton Road ca. 2 miles north of Dales Station on Hwy 36, ca. 14 miles northeast of Red Bluff, T29N, R02W, Sec 26, MD. Elev. 740 ft, locally abundant in gravelly soil. May 20, 1996, *V.H. Oswald and L. Ahart 7613* (JEPS); loc. cit. May 21, 1998, *V.H. Oswald 9087* (JEPS): **NOTES:** Determination by M. Vincent (MU).

*Trifolium stellatum* L.: **DIST:** CCo: **CS:** NCI: **DOC:** Monterey Co.: waif, vacant field, Schilling Company, Salinas. T15S, R03E, Sec. 03, MD. May 31, 1978, *J. Lyons and B. Oliver s.n.* (CDA).

*Trifolium striatum* L.: **DIST:** n SN: **CS:** NCI: **DOC:** Nevada Co.: Grass Valley, East Main Street at Dorsey Drive, waste ground at entrance to Litten Industries complex, T16N, R08E, Sec. 23, MD. June 3, 1980, *G.D. Barbe and P. Hiatt 2791* (CDA, JEPS); Spring Hill between Grass Valley and Nevada City. Elev. 2700 ft. June 19, 1973, *G.H. True 7584* (CAS, CDA); loc. cit. May 11, 1973, *G.H. True 7469 and J.T. Howell* (CAS, CDA); **Sonoma Co.:** Best, C., et al. (1996, pg. 144); Sugarloaf Ridge State Park, ca. 1 air mi S of Red Mtn, Adobe Cyn. T07N, R06W, Sec. 22, MD. May 21, 1996, *F. Bowcutt 2141* (DAV).

*Trifolium tomentosum* Willk. ex Nyman: **DIST:** NCoRO, ScV, SnFrB: **CS:** NW: **DOC:** Contra Costa Co.: Mount Diablo State Park, connector between Barbecue Terrace Road and Wall Point Road, localized patch at edge of path through open oak woodland/grassland. May 3, 1998, *B. Erter 16063* (JEPS); **Napa Co.:** Imola Ave. 0.2 mile west of Suscol Ave., Napa. Grasslands, elev. 20 ft, T05N, R04W, Sec. 14, MD. April 11, 1979, *J. Ruygt 501* (JEPS); **Sacramento Co.:** Pasture adj. to underpass at Rio Linda and SW Elverta, betw. Natomas E Main drain and W end of 'N' St. T10N, R05E, Sec. 19, MD. Elev. 40 ft. May 12, 1992, *R. York 92-002* (CDA); Overflow parking area, E of Cal Expo at Ethan Way, Sacramento. June 7, 1987, *N. Wymer s.n.* (CDA, DAV); **Sonoma Co.:** Best, C., et al. (1996, pg. 144); Annadel State Park, east of Ledson Marsh, several dense patches in grassland, both sides of Marsh Trail, midway between intersection with Lawndale Trail and marsh spillway. April 19, 2000, *A. Howald 2037* (CDA): **NOTES:** Resembling *T. fragiferum* in having the calyx inflated in fruit, but annual and with only a vestigial involucre. All specimens at CDA appear referable to the var. *tomentosum* sensu Zohary and Heller (1984). Easily overlooked and probably more widespread than the collections above indicate.

*Trifolium vesiculosum* Savi: **DIST:** CCo, NCoRO, ScV: **CS:** N: **DOC:** Humboldt Co.: Disturbed road repair area at roadside, Hwy 101 nr Orick. T09N, R01E, Sec. 06, H. Sept. 14, 1998, *P. Haggard s.n.* (CDA); **Santa Cruz Co.:** Common on limestone mine tailings above Davenport. Nov. 26, 2000, *G.F. Hrusa 15725* (CDA); **Solano Co.:** SW of Davis, abandoned fields between Hwy 113 and Pedrick Rd. July 1, 1998, *M. Rejmanek s.n.* (CDA, DAV): **NOTES:** A distinctive species among native and naturalized California clovers, readily distinguished by its chartaceous, inflated calyces having 25+ prominent longitudinal veins and similarly prominent lateral venation. Apparently an occasional component of clover-containing hydro-seed mixtures; Humboldt Co. and

Santa Cruz Co. occurrences may have originated via this pathway.

**Trigonella corniculata** L.: **DIST:** NCoR: **CS:** NCI: **DOC:** **Mendocino Co.:** Ukiah, in cover crop. May 5, 1938, *G.T. Nordstrom* s.n. (UC).

**Trigonella foenum-graecum** L.: **DIST:** CCo, ScV: **CS:** NCI: **DOC:** **Monterey Co.:** Volunteer in vacant field next to Schilling plant, Salinas. T15S, R04E, Sec. 03, MD. April 24, 1979, *B. Oliver* s.n. (CDA); **Yolo Co.:** north edge of Davis just west of B St., weed in barley field. Mar. 27, 1951, *J.M. Tucker* 2058 (DAV, UC).

**Vicia bithynica** (L.) L.: **DIST:** CCo: **CS:** NCI: **DOC:** **Monterey Co.:** waste area, Schilling Co., Salinas. T15S, R04E, Sec. 03, MD. May 15, 1978, *B. Oliver* s.n. (CDA).

#### Fagaceae

**Quercus ilex** L.: **DIST:** SCo: **CS:** N: **DOC:** **Los Angeles Co.:** Claremont, adventive in plantings of chaparral shrubs on grounds of Rancho Santa Ana Botanic Garden, 15 Nov. 1990, *S. Boyd* and *T. Ross* 5305 (RSA, UCR); **Orange Co.:** City of Orange, N end of Yorba St. at Santiago Creek, near Chapman Ave. crossing. Orange 7.5' quad. 33°47'24"N; 117°50'24"W, elev. 260 ft/79 m. Creekbed, several trees to 30 ft. Feb. 1, 2000, *Y. Moore* s.n. (UCR); **Riverside Co.:** Weed tree in a citrus orchard in Rubidoux, area being cleared for houses, but this tree being retained, Oct. 23, 1994, *Donald E. Peck* s.n. (UCR); **Riverside, east side of UCR campus nr. parking lot 13,** assoc. with *Salix lasiolepis*, *Populus fremontii*, *Baccharis salicifolia*, etc. Elev. 335 m/1100 ft. Solitary 5 m tree at edge of wash and parking lot. Clearly spontaneous—no cultivated plants in immediate vicinity. May 12, 1997, *A.C. Sanders* 20711 (UCR); **Riverside, Watkins Dr. east of Blaine St., at Lemona Siding. Riverside East 7.5' quad. 33°58'30"N, 117°19'W; T02S R04W Sec. 20, SB. Elev. 335 m/1100 ft. In hedge of oleander and *Brachychiton* along N side of Watkins. At least 6 young trees, mostly 3–5 m tall, growing as weeds in hedge; plainly spontaneous. May 3, 2001, *A.C. Sanders* 24123 (UCR).**

#### Geraniaceae

**Geranium columbinum** L.: **DIST:** NCo, ScV: **CS:** NCI: **DOC:** **Humboldt Co.:** ca. 7.5 road miles south of Ferndale, along Wildcat Road near Green Pond ranch. May 20, 1987, *Pykala* and *Norris* 751 (MO); **Solano Co.:** 5.6 miles W of Winters. April 16, 1968, *Ishizuka* 19 (MA); **NOTES:** Acc. to Aedo (2000) this is a relative of *G. carolinianum* L., native to the Old World but widely distributed in the northeast US; also in Oregon and Washington.

**Geranium lucidum** L.: **DIST:** SnFrB: **CS:** N: **DOC:** **Alameda Co.:** lower end Strawberry Canyon firetrail behind UC-Berkeley Botanical Garden, locally abundant in wet ground at edge of forest. Apr. 11, 1998, *B. Ertter* 15979 (UC); loc. cit. Apr. 29, 1998, *Ertter* 16029 (UC).

**Geranium purpureum** Vill.: **DIST:** NCoR, SnFrB: **CS:** NW: **DOC:** **Alameda Co.:** lower end of Strawberry Canyon firetrail, behind UC-Berkeley campus. Nov. 23, 1991, *B. Ertter* and *B. Olson* 10891 (UC); loc. cit. Apr. 25, 1974, *L.R. Heckard* 3679 (JEPS); Albany Hill, uncommon at time of collection but rapidly becoming more abundant. May 20, 1995, *B. Ertter* 14216 (UC); corner of Hearst Ave. and Gayley Road, UC-Berkeley campus. Apr. 4, 2001, *B. Ertter* and *D. Norris* 17574 (UC and to be distributed); **Napa Co.:** Kroeber Ranch west of Rutherford, in weed-filled meadow. Apr. 25, 1996, *B. Ertter* and *J. Ruygt* 14601 (UC); **NOTES:** Similar to *G. robertianum*, but with consistently smaller (< 1 cm long), more uni-

formly bright pink petals, yellow (vs. orange) anthers, and less anthocyanic foliage overall.

**Geranium pyrenaicum** Burm. f.: **DIST:** CCo: **CS:** C: **DOC:** **Alameda Co.:** Berkeley Campus, east side of Botany building. June 15, 1914, *W.L. Jepson* s.n. (JEPS); **NOTES:** Current determination by Ertter, 1996; previously determined as (and possibly basis for CCo record of) *G. pusillum* Burm.f. in Hickman (1993).

**Geranium rotundifolium** L.: **DIST:** CCo, SCo, SnFrB: **CS:** NW: **DOC:** **Alameda Co.:** UC-Berkeley campus, in Grinnell Natural Area, locally abundant. June 28, 1996, *B. Ertter* 14910 (UC); Albany Hill. July 13, 1996, *B. Ertter* 14967 (UC); **Contra Costa Co.:** Tilden Regional Park east of Grizzly Peak Boulevard, scattered colonies along dirt road in weedy hillside. May 14, 1996, *B. Ertter* 14684 (UC); **Los Angeles Co.:** Ross, T. and S. Boyd (1996, 435–436); **San Luis Obispo Co.:** Huasna Rd., 1.5 rd miles E of bridge over Huasna River; foothill woodland and chaparral patches, area grazed. Occasional on roadside. April 1, 1995, *D. Keil* 24714 (OBI); US 101 1.3 miles NW of Cuesta Pass, ca. 0.4 miles S of Tassajara Creek Rd.. Coastal live oak woodland and adjacent roadside zone, locally common in roadside zone and edge of woodland understory. May 27, 1999, *D. Keil* 28354 (OBI); Cuesta Grade East along Mt. Lowe Rd., ca. 2 road miles from Highway 101, locally common under shade of *Quercus agrifolia* on bank above road. May 9, 2000, *D. Keil* 28648 (OBI); **NOTES:** Somewhat reminiscent of *Geranium molle*, but with entire (vs. apically notched) petals, a short awn (< 1 mm long) on the sepals, fruits that are finely hairy rather than wrinkled, and less deeply lobed leaves. Noted as weed elsewhere in Berkeley; possibly seen by Ertter on Fremont Peak, **San Benito Co.**

**Geranium texanum** (Trel.) A. Heller: **DIST:** CCo: **CS:** NCI: **DOC:** **Marin Co.:** Aedo (2000); Olema. June 7, 1936, *Howell* s.n. (NY); **NOTES:** This species, another relative of *G. carolinianum* L., otherwise occurs in east Texas and Louisiana (and the Azores). According to Aedo (2000), "Its presence in California (not previously recorded) probably constitutes a[n] occasional introduction".

#### Hamamelidaceae

**Liquidambar styraciflua** L.: **DIST:** ScV: **CS:** TEN: **DOC:** **Sacramento Co.:** North bank of American River, American River Parkway, a few hundred meters downriver of the Estates Dr. entrance. 38°33'N; 121°22'W. June 16, 1998, *J. Randall* s.n. (CDA, DAV).

#### Hydrophyllaceae

**Wigandia caracasana** HBK.: **DIST:** SCo: **CS:** NCI: **DOC:** Munz, P.A. (1974, pg. 519); **NOTES:** No evidence for naturalization. Labeled specimens at CDA collected in the locations cited by Munz (1974), state that the plants were cultivated but without mention of spread from root-sprouts or other persistence mechanisms. Because this plant has an extensive root system it is a likely candidate to remain persistent from cultivation and spread locally.

#### Hypericaceae

**Hypericum androsaemum** L.: **DIST:** SnFrB: **CS:** N: **DOC:** **Alameda Co.:** Strawberry Creek behind UC-Berkeley Botanical Garden, June 16, 1993, *B. Ertter* 11898 (UC).

**Hypericum calycinum** L.: **DIST:** CCo, SnFrB: **CS:** TEN: **DOC:** **Contra Costa Co.:** Berkeley-Oakland Hills, Grizzly Peak Boulevard ca. ¼ miles south of Lomas Can-

tadas junction, dense patch on east side of road at edge of mixed scrub, elev. ca. 100 ft. June 25, 1993, *B. Ertter 11907* (UC); **San Francisco Co.**: Howell, J.T. et al. (1958, p. 102); Thomas, H. (1961, p. 239); **NOTES**: Gen. spreading vegetatively in California where it is widely planted and often persistent. Fully naturalized and spreading by seed in Oregon and Washington States, but similar behavior not confirmed in California.

***Hypericum hookerianum* Wight & Arn.**: **DIST**: NCo: **CS**: **TEN**: **DOC**: **Mendocino Co.**: forest road near Little North Fork Gualala River and Doty Creek, UTM Zone 10, 4298N, 4550E, elev. 100 ft, one large patch in second growth redwood forest, shrub 1–2 m tall. July 8, 2000, *G. Leppig 1453* (CDA, HSC); **Santa Barbara Co.**: Montecito, Montecito School for Girls, escape from cultivation. June 9, 1951, *H.M. Pollard s.n.* (DAV, SBBG), det. by J.T. Howell.

#### Lamiaceae

***Calamintha sylvatica* Bromf. subsp. *ascendens* (Jordan) P.W. Ball**: **DIST**: SnFrB: **CS**: **TEN**: **DOC**: **Alameda Co.**: Strawberry Canyon northeast of Panoramic Place in Oakland-Berkeley Hills, roadcut below oak forest, small persisting patches at two sites along fire road. Sept. 2, 2000, *B. Ertter 17518* (UC); **NOTES**: Nomenclature as in *Flora Europaea*, which uses a narrow circumscription of *Satureja*. If the same generic circumscriptions were applied in North America, no native *Satureja* would occur in California. An alternate name for this taxon is *Satureja calamintha* (L.) Scheele subsp. *ascendens* (Jordan) Briq. This is apparently the first record of the species occurring spontaneously in North America, although the closely related *C. nepeta* (L.) Savi is widely established in eastern North America.

***Cedronella canariensis* (L.) Willd. ex Webb & Berth.**: **DIST**: CCo: **CS**: **NCI**: **DOC**: **San Francisco Co.**: Howell, J.T. et al. (1958, p. 119); Thomas, H. (1961, p. 299); Jepson, W.L. (1943, pg. 400); Mud Lake, vicinity of San Francisco Bay. July 1914, *A. King s.n.* (JEPS).

***Galeopsis tetrahit* L.**: **DIST**: MP: **CS**: **NCI**: **DOC**: **Modoc Co.**: Corporation Ranch, Likely. July 8, 1958, *T.C. Fuller 1973* (CDA); Pit River Valley south of Alturas, irrigation ditch near S end of west side road, roadside. July 12, 1947, *H.L. Mason and V. Grant 13417* (DAV, UC).

***Lamiastrum galeobdolon* (L.) Ehrend. & Polatsch.**: **DIST**: NCo: **CS**: **TEN**: **DOC**: **Humboldt Co.**: Arcata, Arcata Community Forest, 100 m S of trails 5 and 10 intersection. Second growth redwood forest. Large stoloniferous mat. April 13, 2000, *G. Leppig 1292*, *K. Neander* (CDA, HSC); **NOTES**: Single 1/10 ha. patch. Represented here by a variegated cultivar, also sold as *Lamium galeobdolon* or *Lamium variegatum*.

***Lavandula stoechas* L.**: **DIST**: CCo, NCo: **CS**: **C**: **DOC**: **Alameda Co.**: sidewalk crack on Shattuck Ave. nr. Lincoln St. north Berkeley. June 25, 2001, *B. Ertter 17699* (UC); **Sonoma Co.**: Fuller Mountain Rd., nr. summit of Fuller Mtn., occasional on roadside in mixed conifer forest. April 22, 2000, *G. Leppig 1311* (CDA, HSC).

***Mentha × villosa* Huds.**: **DIST**: SnFrB: **CS**: **NCI**: **DOC**: **Napa Co.**: Napa River riparian zone on gravel bar with willows, ca. ½ mile north of Trancas Street, city of Napa. El. 10 ft, T06N, R04W, Sec. 34, MD. Napa 7.5' quad. Sept. 25, 1989, *J. Ruygt 2408* (UC).

***Monarda citriodora* Cerv.**: **DIST**: ScV: **CS**: **N**: **DOC**: **Sacramento Co.**: roadside, Jackson Rd. (Hwy 16) W of Eagles Nest Rd. T08N, R06E, Sec. 25, MD. Elev. 125 ft.

July 17, 1997, *F. Carl s.n.* (CDA); loc. cit. August 15, 1997, *G.D. Barbe 4478* (CDA).

***Rosmarinus officinalis* L.**: **DIST**: CCo, SCo: **CS**: **C**: **DOC**: **Alameda Co.**: Albany waterfront, on former landfill, several local shrubs. Aug. 19, 1994, *B. Ertter 13077* (UC); **Orange Co.**: Newport Bay, North Star County Beach area on the SW end of the bay, ca. 2 km inland of Hwy 1, clearly spontaneous, not planted. Oct. 6, 1990, *A.C. Sanders 10202* (DAV, UCR); **NOTES**: Single mature shrub also persisting near Huckleberry Regional Botanical Area, **Alameda Co.**, spontaneous?

***Salvia longistyla* Benth.**: **DIST**: CCo: **CS**: **N**: **DOC**: **Monterey Co.**: Locally but abundantly spontaneous on bank of Big Sur River at Big Sur. Apr. 13, 1961, *J.T. Howell 36487* (CAS, CDA); Munz, P.A. (1968, pg. 103); Howitt, B.F. and J.T. Howell, (1973, pg. 29); **NOTES**: Cited on pg. 1343 of the Jepson Manual as "not naturalized"; however field observation reports it extant and vigorous in 2000, acc. to G. Norman via M.A. Matthews (personal communication to Hrusa, 4-2000).

***Salvia microphylla* Benth.**: **DIST**: CCo, NCoRO, SCo: **CS**: **NCI**: **DOC**: **Marin Co.**: Howell, J.T. (1970, pg. 358); **Monterey Co.**: Matthews, M.A. (1997, pg. 179); Coal Chute Pt., dry sunny loam, originally cult. Aug. 14, 1936, *L.B. Wheeler 4369*. (Point Lobos State Reserve Herbarium); **Santa Barbara Co.**: Munz, P.A. (1968, pg. 704); **Sonoma Co.**: Best, C., et al. (1996, pg. 164); **NOTES**: Cited on pg. 1343 of the Jepson Manual as "not naturalized" under the name *S. grahamii* Benth.

***Salvia reflexa* Hornem.**: **DIST**: CaRF, SNE: **CS**: **GH**: **C**: **DOC**: **Inyo Co.**: garden in Independence, Rosedale Dr., elev. 4000 ft. July 24, 1996, *M. DeDecker 6559* (CDA, RSA); **Shasta Co.**: garden of residence at 3657 Encanto Way northeast of Redding, surrounded by blue oak woodland. May 16, 1993, *B. Ertter 11837* (UC).

***Salvia virgata* Jacq.**: **DIST**: MP, SBr., n SN: **CS**: **NCI**: **DOC**: **Nevada Co.**: just east of Grass Valley, on Empire Mine property. July, 1972, *L. Mott s.n.* (JEPS); Empire Mine property, end of Stacy Lane off Highway 49, south side of Grass Valley, T16N, R08E, Sec. 34, MD. Weedy in 2-acre meadow. June 8, 1972, *T.C. Fuller and G.D. Barbe 964* (CDA, UC), det. by Ian C. Hedge (RGBE), Feb. 1987; **San Bernardino Co.**: Lake Arrowhead, garden escape. Aug., 1931, *Braunton 1056* (DS); **Siskiyou Co.**: scattered plants on 600 sq. ft of drainage way in dry rangeland, adjacent to wet slough, Greenhorn Valley, ca. 2 mi W of Yreka. June 24, 1964, *T.C. Fuller 12244* (CDA), det. by E. McClintock; loc. cit. July 29, 1968, *C.S. Giebner s.n.* (CDA); Ager Beswick Road, very dry roadside. Aug., 1998, *L. Parsons s.n.* (JEPS); **NOTES**: Extirpated in Nevada Co.; status of Siskiyou Co. plants currently under investigation. San Bernardino Co. specimen originally identified as *Salvia pratensis* L. (*sensu stricto*). Acc. to R. Breckenridge (CDFA, Integrated Pest Control Branch), *Salvia virgata* is readily distinguished from *S. pratensis* s.s. by the foetid odor of its foliage.

***Scutellaria caerulea* M. & S.**: **DIST**: CCo: **CS**: **C**: **DOC**: **Santa Clara Co.**: Weed in commercial field herb crop in Gilroy. Rocket Farms. Sept. 20, 1999, *K. Meyer s.n.* (CDA), det. by G.F. Hrusa (UC).

***Stachys floridana* Shuttlew.**: **DIST**: ScV: **CS**: **GH**: **C**: **DOC**: **Sacramento Co.**: Abundant in garden, 2424 Park Estates Dr., Sacramento. May 21, 1963, *K.S. Buchanan s.n.* (CDA); loc. cit. June 7, 2000, *L. Manger s.n.* (CDA); **NOTES**: Tuberous perennial, spreading by rootsprouts. Present at this locality for at least 37 years.

## Lauraceae

***Cinnamomum camphora* (L.) J. Presl:** **DIST:** deltaic GV: **CS:** C: **DOC:** **Contra Costa Co.:** Antioch National Wildlife Refuge, Stamm Unit, two juvenile individuals on riparian margin, apparently spontaneous but source not evident. May 26, 2001, *B. Ertter et al.* 17563 (UC): **NOTES:** A fairly common landscape volunteer, but seedlings generally restricted to irrigated sites and seldom allowed to mature.

***Laurus nobilis* L.:** **DIST:** CCo, NCo: **CS:** TEN: **DOC:** **Humboldt Co.:** Arcata, occasional in disturbed empty lot in redwood forest. Trees 2–4 m tall. April 12, 2000, *G. Leppig* 1289 (CDA, HSC); **San Francisco Co.:** Howell, J.T. et al. (1958, pg. 73); Thomas, H. (1961, pg. 173): **NOTES:** Single plant persisting on Albany Hill, **Alameda Co.,** from unknown source and origin.

## Lentibulariaceae

***Utricularia subulata* L.:** **DIST:** NCoRO: **CS:** NCI: **DOC:** **Mendocino Co.:** Meyers-Rice (Madrono, in press); spreading through wet depressions and seeps in a pygmy forest, 39°15'N; 123°45'W. Nov. 2, 1997, *B. Meyers-Rice* #MR971102 (DAV): **NOTES:** Intentionally introduced.

## Limnanthaceae

***Limnanthes macounii* Trel.:** **DIST:** CCo: **CS:** N: **DOC:** **San Mateo Co.:** Buxton (1998, pg. 184); Along east side of Hwy 1 south of Moss Beach, directly opposite Half Moon Bay airport, in cultivated field. Elev. ca. 10 m. Feb. 24, 2000, *R. Schmid* 2000-2 (UC): **NOTES:** Unclear whether a locally naturalized alien or a previously overlooked native.

## Linaceae

***Linum trigynum* L.:** **DIST:** NCo: **CS:** NCI: **DOC:** **Sonoma Co.:** Best, C., et al. (1996, pg. 168).

## Malvaceae

***Anisodontea capensis* (L.) Bates:** **DIST:** NCoRO, ScV: **CS:** C: **DOC:** **Sonoma Co.:** Best, C., et al. (1996, pg. 171); **Sacramento Co.:** Among landscape shrubs along sidewalk in Sacramento. July 10, 2000, *R. Gill* s.n. (CDA): **NOTES:** In the nursery trade as *Malvastrum capense* (L.) Gray & Harv. and so reported for Sonoma County (Best et al., 1996).

***Anoda pentaschista* A. Gray:** **DIST:** DSon: **CS:** NCI: **DOC:** **Imperial Co.:** Weed in citrus, nr Bard. Sept. 9, 1983, *L. Pineda* s.n. (CDA).

***Gossypium hirsutum* L.:** **DIST:** DSon, ScV: **CS:** NCI: **DOC:** **Imperial Co.:** Two ruderal plants betw. rd and base of canal bank, N side Hwy 98 to Mt. Signal 1.7 mi W of Calexico. Oct. 18, 1962, *T.C. Fuller* 9804 (CDA); **Sacramento Co.:** City of Sacramento, Tahoe Park neighborhood, near the old fairgrounds, volunteer. Sept. 18, 1995, *D. Goosen* s.n. (DAV).

***Hoheria populnea* A. Cunne.:** **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Voluntary in dwarf conifer area, Strybing Arboretum, Golden Gate Park, San Francisco. Sept. 20, 1973, *G. Beutler* s.n. (CDA).

***Lavatera olbia* L.:** **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Shrubs to 8 ft tall, commonly naturalized on non-irrigated waste ground of formerly cultivated garden, Stanyon St., San Francisco. Aug. 4, 1970, *T.C. Fuller* s.n. (CDA).

***Lavatera trimestris* L.:** **DIST:** SCo: **CS:** NCI: **DOC:**

**Santa Barbara Co.:** Smith, C.F. (1976, pg. 192); Edge of water, Lauro Canyon Reservoir nr. San Roque Rd., Santa Barbara. June 25, 1975, *C. Smith and J.L. Johnson* s.n. (CDA).

***Malva verticillata* L.:** **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co., Ventura Co.:** Smith, C.F. (1976, pg. 193).

***Sida spinosa* L.:** **DIST:** SnJV: **CS:** NCI: **DOC:** **Fresno Co.:** near Sanger by the Ciba-Geigy Research Station on Annadale Ave., ca. ¼ mi W of Reed Ave. Aug., 1996, *B. Fischer* s.n. (DAV).

## Moraceae

***Fatoua villosa* (Thunb.) Nakai:** **DIST:** SCo, SnJV: **CS:** GH/C: **DOC:** **Kern Co.:** Greenhouse weed, Arvin. Oct. 19, 1998, *Lapp et al.* s.n. (CDA); **Riverside Co.:** Sanders, A.C. (1996, pg. 527); **San Bernardino Co.:** Ontario. Weedy throughout nursery, under benches, in walkways. Oct. 21, 1983, *Cohen* s.n. (CDA); **San Diego Co.:** Nursery containers, greenhouse, Fallbrook. Feb. 14, 1985, *F. McCutcheon* s.n. (CDA): **NOTES:** Also confirmed, but not vouchered, from **Tehama Co.,** in commercial greenhouses. Similar vegetatively to species of *Laportea* (Urticaceae) and has been reported as that genus. Seed form readily distinguishes *Fatoua* from *Laportea*.

***Ficus palmata* Forssk.:** **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Spontaneous in creekbed, W Fk. Cold Spring Cyn., Santa Barbara. Dec. 23, 1958, *H.M. Pollard* s.n. (CAS, CDA): **NOTES:** Cited in Munz (1974) Smith, C.F. (1976) and Rejmanek and Randall (1994) as *F. pseudocarica* Miq.

## Nymphaeaceae

***Nymphaea alba* L.:** **DIST:** NCo: **CS:** NCI: **DOC:** **Mendocino Co.:** Smith, G. and C. Wheeler (1990–1991, pg. 150).

## Oleaceae

***Fraxinus uhdei* (Wenz.) Lingel.:** **DIST:** SCo: **CS:** NW: **DOC:** **Los Angeles Co.:** "Cottonwood Swamp", confluence of San Francisquito Canyon stream and two tributaries draining off the southeast slopes of Red Mountain. Warm Springs Mtn. 7.5' quad., T05N, R16W, Sec. 01, elev. 1680–1690 ft [possible hybrid]. *T.S. Ross* 7835 ((RSA? UCR, UC); **San Bernardino Co.:** Colton, S Pelisier Rd., near the corner of W Center St. and Orange St., 34°01'13", 117°20'55"W. T02S, R05W, SB. Elev. 262 m. Ephemeral creek with sandy bottom and the shaded grassy slopes above it. Nr. historical settlement. Associated with *Populus fremontii*, *Juglans californica* and *Rubus discolor*. Solitary sapling. Apr. 4, 1999, *Mitch Provance* 1763 (UCR): **NOTES:** Widespread and sometimes locally common in coastal southern California riparian zones. For example, along the Santa Ana River near Riverside it forms a conspicuous element of the tree canopy near the confluence of Spring Brook. Where street runoff flows into permanently moist riparian areas, this species usually appears. Identification is confused by the fact that it seems to hybridize with the *F. velutina* Torr. (*F. pennsylvanica* Marsh) complex, including both native plants and cv. 'Modesto.' Easiest to identify in winter because it is evergreen, unlike the others. Much was cut last year in the area around Haskell Creek in the Sepulveda Basin during an effort to control exotics. Acc. to John Eckhoff (personal communication to Sanders), they are "finding this tree in many of the riparian areas we visit or find ourselves

working in, like San Gabriel River and Big Tujunga Wash at the base of the San Gabriel Mts.". Voucher requested but not received.

**Ligustrum lucidum** W.T. Aiton: **DIST:** NCoRO, ScV, SnBr, SCo: **CS:** NW: **DOC:** **Riverside Co.:** Riverside, weed tree in landscaping on UCR campus, elev. 1100 ft. Dec. 16, 2000, A.C. Sanders 23728 (UCR); **Sacramento Co.:** Quinn, J., et al. (1991); **San Bernardino Co.:** San Bernardino Mtns., Thurman Flats Picnic Area, below Mountain Home Village, Yucaipa 7.5' quad., T01S, R01W, Sec. 08, SB, 34°06'30"N; 117°00'05"W, elev. 3480 ft/1061 m, dense alder forest along the stream; solitary small tree ca. 3 m high in forest understory. May 27, 2000, A.C. Sanders 23432 (UCR); **NOTES:** This species is scattered around as an urban weed tree in the Riverside area; seeds apparently dispersed by birds. Also observed by Hrusa as seedlings and young trees in riparian zone along Arcade Cr., N side Interstate 80, Sacramento Co.; also by J. Ruygt (pers. comm., 3-2001), as seedlings on Redwood Rd., ca. 0.5 mi W of Hwy 29, and as seedlings and adult trees along bank of Camille Cr. At Polley Drive, both near Napa in **Napa Co.** Seldom collected, but apparently widespread in moist habitats.

**Ligustrum ovalifolium** Hassk.: **DIST:** CCo, NCo, ScV: **CS:** NW: **DOC:** **Mendocino Co.:** Sinkyone Wilderness State Park, old homesite 2.7 miles south of Needle Rock Ranch House. Lost Creek trailhead in red alder woodland. June 25, 1995, F. Bowcutt 2009 (DAV, HSC); Rt. 1 near entrance to McKerricher State Park. Self-sustaining for over 50 years. July 30, 1981, G. L. Smith and C. R. Wheeler 7205 (HSC). **Monterey Co.:** Elkhorn Slough National Estuarine Research Reserve, disturbed fields near South Marsh. May 22, 2000, G. Leppig 1382 (HSC); **Sacramento Co.:** Quinn, J., et al. (1991); **NOTES:** Known sites highly localized.

**Olea africana** Mill.: **DIST:** SCo: **CS:** TEN: **DOC:** **Riverside Co.:** Riverside, Mt. Rubidoux, NE foot of the mountain above the end of 9th St., 33°59'N; 117°23'W, T02S, R02W, Sec. 22, SB. Elev. 1000 ft/305 m, E-facing decomposed granite slopes at edge between landscaped (residential) areas and coastal sage scrub. Disturbed and weedy with some no longer tended ornamentals. A locally common shrub or tree to 10 m tall. Oct. 23, 1996, A.C. Sanders 19643 (UCR); **NOTES:** Some individuals probably originally planted (persisting ornamentals), but others growing in cracks of boulders, etc. and plainly spontaneous. This is so scarce as a cultivated plant that this might easily be the only naturalized locality, where it is doing well. Reproduction is apparently by seed.

#### Onagraceae

**Fuchsia magellanica** Lam.: **DIST:** CCo, NCo: **CS:** NW: **DOC:** **Contra Costa Co.:** Cerrito Creek west of San Pablo Avenue, several reproducing shrubs on stream bank. Sept. 17, 1999, B. Ertter 16845 (UC); **Humboldt Co.:** Low shrub naturalized at base of *Alnus* sp., loop trail above Fern Canyon, Prairie Ck. Redwood State Park, 7.1 mi W of Highway 101 on Fern Canyon Rd. June 18, 1974, G.D. Barbe 1872 (CDA); **Mendocino Co.:** Mendocino, edge of headland behind Presbyterian church, uncommon shrub mixed in willow thicket. Sept. 29, 1992, B. Ertter 11449 (UC); **Monterey Co.:** Carmel Highlands, Fern Canyon east of Highway 1, shade of pine forest along creek. June 13, 1993, B. Ertter, V. Yadon, and M.A. Matthews 11890 (UC); Gibson Canyon, near Carmel Highlands. Growing in moist cyn. bottom, 6–10 pls. over several hundred yds, 600 ft elev. June 13, 1994, D. Kelch s.n.

(DAV); **San Francisco Co.:** Lobos Creek between Lincoln Blvd. and Baker Beach, deep shade. Nov. 15, 1992, B. Ertter 11459 (UC); **NOTES:** Some individual sites may be considered tenuous (TEN). Label data for second Mendocino Co. site in Sinkyone Wilderness State Park, [old home sites. T24N, R19W, Sec. 26, MD. May 23, 1989, F. Bowcutt 1325 (DAV)], are not clear that location is spontaneous.

**Fuchsia × hybrida** Voss.: **DIST:** SCo: **CS:** NCI: **DOC:** **Ventura Co.:** Persisting or spontaneous (?) in a clump of *Ricinus* shrubs on SPRR right of way, east Ventura. June 1, 1961, H.M. Pollard s.n. (CDA).

#### Orobanchaceae

**Orobanche hederæ** Duby: **DIST:** CCo: **CS:** TEN: **DOC:** **Alameda Co.:** UC-Berkeley campus, small persisting colony in *Hedera* groundcover next to Koshland Hall. June 7, 2000, B. Ertter 17310 (UC); between student center and Alumni House. May 8, 2001, B. Ertter 17626 (UC).

#### Papaveraceae

**Fumaria capreolata** L.: **DIST:** CCo, SnFrB: **CS:** N: **DOC:** **Alameda Co.:** Landscape weed in Livermore area. March 9, 1994, C. Elmore s.n. (DAV); **Contra Costa Co.:** Miller Knox Regional Park, at edge of excavation on west-facing hillside, localized but dense colony at base of coast live oak. Mar. 21, 1999, B. Ertter 16486 (UC); **Marin Co.:** Muir Beach, 5.5 miles west of Hwy 1. Open area, slightly sandy soil, coastal strand with partial moisture, full sun. Not abundant. Elev. 50 ft. May 16, 1992, J.N. Le 17 (DAV); **San Francisco Co.:** Spontaneous along path betw. the Conservatory and Fuchsia garden, Golden Gate Park, San Francisco. Sept. 25, 1980, J.T. Howell 53901 (DAV); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 135); **NOTES:** Known sites widely scattered. Differing from the other naturalized species of *Fumaria* in California in the larger flowers (ca. 12 mm long) and broadly ovate sepals. Apparently becoming more common. Similar to *F. macrosepala* Boiss. which may also be represented in California (Ertter 16486).

**Papaver × hybridum** L.: **DIST:** CCo, ScV, SnJV: **CS:** NCI: **DOC:** **Kern Co.:** Point of Rocks, western (Kern) County. Apr. 27, 1950, E. McMillan and C. Smith 2684 (DAV); Antelope Valley, 3 mi W of Point of Rocks, the probable origin of the plants, not previously observed here by local farmers. Apr. 8, 1962, E. Twisselmann 6770 (CDA, DAV); **Madera Co.:** E side of Rd 26, 0.1 mi S of Ave. 12, 1 mi W of Madera, dominant weed on one acre of newly planted vineyard. Apr. 6, 1967, J.S. Davis s.n. (CDA); loc. cit. Apr. 19, 1967, T.C. Fuller 15609 (CDA, DAV); **Sacramento Co.:** SW corner of Metropolitan Airport property near Garden Highway. Apr. 4, 1992, K. Miller s.n. (CDA, DAV); **San Luis Obispo Co.:** Choice Valley Hills, SE side of Sinsheimer Flat, dense colony in a bare area in a dry-farm wheat field (barley field in 7027). Apr. 29, 1962, E. Twisselmann 7025, 7027 (CDA, DAV); **NOTES:** The Twisselmann and J.S. Davis specimens were originally determined as *Papaver apulum* Ten. var. *micranthum* (Bor.) Fedde. Comment by Twisselmann indicated it is recent in San Luis Obispo Co.

#### Passifloraceae

**Passiflora caerulea** L.: **DIST:** NCoR, SnGb, SCo, s: **SN:** **CS:** N: **DOC:** **Los Angeles Co., Riverside Co. and San Bernardino Co.:** Sanders, A.C. (Madrono, in press);



**Fresno Co.:** Sequoia Mills, no date, *K. Brandegee s.n.*, (UC); **Napa Co.:** Calistoga, July 11, 1910, *K. Brandegee s.n.* (UC); **NOTES:** Long persisting and difficult to eradicate in garden situation, indicating strong potential to naturalize. Serves as host plant for non-native gulf fritillary caterpillars. Reported as non-spontaneous in Ventura Co. by H.M. Pollard (specimen at DAV, SBBG).

***Passiflora manicata* (Juss.) Pers.:** **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Smith, C.F. (1976, pg. 197).

***Passiflora mixta* L. f.:** **DIST:** CCo: **CS:** N: **DOC:** **San Francisco Co.:** Golden Gate Park, local patch at junction of Crossover Drive and John F. Kennedy Drive. Sept. 11, 1993, *B. Erter 12269* (UC); **NOTES:** *Passiflora mollissima* auct. non (Kunth) L.H. Bailey as discussed under *P. tarminiana*. Freely reseeding in garden situation on Catalina Ave., Berkeley (**Alameda Co.**).

***Passiflora tarminiana* Coppens & Barney:** **DIST:** CCo: **CS:** N: **DOC:** **Contra Costa Co.:** edge of vacant lot at SW corner of San Pablo Avenue and Carlson Ave., climbing on *Sambucus* at edge of Cerrito Creek. Sept. 17, 1999, *B. Erter 16846* (UC); **NOTES:** Observed by Erter to be also established upstream near BART path. Seedlings occasionally encountered (and eliminated) by Erter on Albany Hill, near Cerrito Creek. population; Reported also from Riverside Co. All original determinations as *Passiflora mollissima* auct. non (Kunth) L.H. Bailey, current determinations by D. Goldman. See Novon 11(1): pg. 9, 2001, for more information. Potentially a noxious pest, as in Hawaii (as *P. mollissima* sensu auct.), where capable of smothering native forests.

Pedaliaceae

***Sesamum indicum* L.:** **DIST:** ScV, SNF: **CS:** C: **DOC:** **Mariposa Co.:** Few plants along roadside, Hwy 140 nr. Cathays Valley. Aug. 30, 1978, *K.A. Parker s.n.* (CDA); **Sacramento Co.:** Single plant in asphalt divider, Kiefer Blvd, nr. Bradshaw Rd. Aug. 30, 1977, *K. Miller s.n.* (CDA); **NOTES:** Occurrences probably originating via commercial bird seed.

Plumbaginaceae

***Limonium ramosissimum* (Poir.) Maire subsp. provinciale (Pignatti) Pignatti:** **DIST:** SCo: **CS:** NW: **DOC:** **Santa Barbara Co., Ventura Co.:** From Rick Burgess garden in Oxnard; originally collected in Carpenteria Salt Marsh, where it has naturalized about its mouth and is a very serious problem. 1994, *Rick Burgess s.n.* (SBBG); **NOTES:** Apparently from garden plants in an adjacent subdivision. Data provided by Dieter Wilken (SBBG).

Polygalaceae

***Polygala myrtifolia* L.:** **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Smith, C.F. (1976, pg. 183).

Polygonaceae

***Polygonum multiflorum* Thunb.:** **DIST:** SnFrB: **CS:** GH/C: **DOC:** **Marin Co.:** Rampant weed in garden of Margadant Hayakawa, Eldridge Ave, Mill Valley. Vigorously spreading, but does not flower. Jan. 15, 1976, *M. Hayakawa s.n.* (CDA), det. by E. McClintock, 9/1977; Cultivated in greenhouse [from roots dug at site of previous collection], 3294 Meadowview Rd., Sacramento. Nov. 21, 1980, *G.D. Barbe 3023* (CDA); **NOTES:** Dried tubers of this species ('Fo-ti' or 'Ho Shou-wu') are used as a folk remedy (Tyler 1982).

***Polygonum orientale* L.:** **DIST:** SCo, ScV: **CS:** C: **DOC:** **Sacramento Co.:** spontaneous in residential yard, 2458 Catalina Dr. Sacramento. Aug. 11, 1975, *F. Hine s.n.* (CDA); **Santa Barbara Co.:** Smith, C.F. (1976 pg. 122); **NOTES:** A specimen labeled only as "Mendocino Co., July 25, 1958, *T. Erickson, Jr. s.n.*" is at CDA, but spontaneity unknown. Other known occurrences are fugitives from cultivation.

Ranunculaceae

***Caltha palustris* L.:** **DIST:** CCo, NCoR, NCo: **CS:** NW: **DOC:** **Alameda Co.:** Oakland Hills, Canyon east of Skyline Blvd, growing in stream that separates Huckleberry Preserve from Sibley Volcano Park, along Skyline trail, nr. old homestead site. May 1, 1993, *E.A. Dean 359* (DAV); **Mendocino Co.:** Smith, G. and C. Wheeler. (1990–1991, pg. 151–152). **Sonoma Co.:** Rubtsoff, P. (1959, pp. 31–32); **NOTES:** Rubtsoff record also reported in Best, C., et al. (1996, pg. 201).

***Clematis terniflora* DC.:** **DIST:** ScV: **CS:** TEN: **DOC:** **Sacramento Co.:** Invasive in residential landscape and adjacent field on Larkspur Lane in Citrus Heights. Both sites relatively moist, both with sunny and shady situations. Climbing in *Populus fremontii* to 40+ ft, also in lower borders. Apr. 28, 2000, *G.F. Hrusa 15389* (CDA); **NOTES:** Origin of infestation uncertain, but may have originated as garden ornamental. First noted as a pest in this site in 1992. Owners are attempting extirpation.

***Clematis vitalba* L.:** **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, pg. 72); Thomas, H. (1961, pg. 169); **NOTES:** Volunteer from planted material in Strybing Arboretum, Golden Gate Park, San Francisco.

***Nigella damascena* L.:** **DIST:** SnFrB, NCoRO: **CS:** N: **DOC:** **Contra Costa Co.:** waste ground, Brentwood Road at SPRR tracks, Brentwood. T01N, R02E, Sec. 18, MD. June 18, 1974, *J. deFremery and C. Butler s.n.* (CDA); **Sonoma Co.:** Best, C., et al. (1996, pg. 203); **NOTES:** Garden escape, naturalized as a weed about habitations.

***Ranunculus cortusifolius* L.:** **DIST:** CCo: **CS:** TEN: **DOC:** **Alameda Co.:** Berkeley, University of California campus, untended garden plots at NW corner of Valley Life Sciences Building. May 8, 2001, *B. Erter 17625* (UC); **NOTES:** Possibly originating from deliberately strewn seeds, but now self-sustaining and spreading to adjacent untended plots. Determination by R. Ornduff. 2000.

Rhamnaceae

***Ziziphus jujuba* L.:** **DIST:** ScV: **CS:** C: **DOC:** **Sacramento Co.:** Ditch at corner Sheldon Rd and Hwy 99, sapling. July 7, 1998, *N. Wymer s.n.* (CDA); **Yolo Co.:** 15–20 plants up to 1 meter tall on W side of Hwy 113 appr. 1 mi N of Covell exit in Davis. Obviously spontaneous, some inside ROW. Aug. 21, 2001, *D. Adams s.n.* (CDA); **NOTES:** Escape from cultivation, perhaps from garden trash.

Rosaceae

***Cotoneaster lacteus* W.W. Smith:** **DIST:** CCo, SnFrB: **CS:** NW: **DOC:** **Alameda Co.:** Albany Hill, scattered colony. Feb. 9, 1997, *Erter 15449* (UC); **Contra Costa Co.:** Ygnacia Valley Road cut through Lime Ridge, single shrub. Jan. 5, 1997, *Erter 15432* (JEPS); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 144); **NOTES:** Noted elsewhere in the east San Francisco Bay Area. Flowers

like *C. pannosus* but leaves larger, 3.5–7 cm long, obviously depressed-veiny, obovate-elliptic with obtuse apex; inflorescence often more floriferous as well.

***Crataegus monogyna* Jacquin.** **DIST:** NCoRO, SnFrB: **CS:** NW: **DOC:** Alameda Co.: Dry Creek/Pioneer Regional Park east of Hayward. Jan. 19, 1992, *B. Ertter 10894* (UC); Anthony Chabot Regional Park, Cascade Trail. April 29, 1981, *Jack Stratford s.n.* (JEPS); also observed by Ertter as well-established in Sibley Volcanic Regional Preserve, Oakland Hills; **San Mateo Co.:** McClintock, E., et al. (1990, pg. 102): **NOTES:** Also observed as widely scattered plants on the Palisades, south shoulder of Mt. St. Helena in **Napa Co.** Thorny shrub to small tree, leaves 3–5-lobed halfway or more to midvein.

***Cydonia oblonga* Mill.** **DIST:** ScV, SCo, SnJV: **CS:** NCI: **DOC:** Sacramento Co.: bush 10 ft tall and across, one of a number of plants persistent from cult. in a fence-row, W side of Elk Grove-Florin Rd., 0.1 mi N of Sheldon Rd., Elk Grove. Nov. 19, 1969, *T.C. Fuller 19101* (CDA); **Santa Barbara Co.:** Smith, C.F. (1976, p. 160); **Stanislaus Co.:** ¼ mi W of La Grange, Nof Hwy 132, woodland at edge of dredge tailings, occasional escape in this area. April 3, 1969, *P. Allen 123* (DAV): **NOTES:** Sacramento County site now in developed area, probably extirpated.

***Cydonia sinensis* Thouin.** **DIST:** NCo: **CS:** NCI: **DOC:** Mendocino Co.: Smith, G. and C. Wheeler, (1990–1991, pg. 181): **NOTES:** Reported as *Chaenomeles sinensis* (Thouin) Koehne.

***Eriobotrya japonica* Lindl.** **DIST:** SnFrB, SCo: **CS:** NCI: **DOC:** Alameda Co.: Oakland, Joaquin Miller Park, Sunset Trail. Occasional in redwood forest. Dec. 4, 2000, *G. Leppig 1521* (HSC); **Santa Barbara Co.:** Smith, C.F. (1976, p. 160): **NOTES:** Seedling observed on Albany Hill (Alameda Co.) by Ertter. Expected elsewhere.

***Filipendula vulgaris* Moench.** **DIST:** SnFrB: **CS:** NCI: **DOC:** Alameda Co.: few scattered plants uphill from Australasian beds, Univ. of California Botanic Garden, Strawberry Canyon, Berkeley. Oct. 12, 1978, *G.D. Barbe 2459* (CDA).

***Photinia davidsoniae* Rehd. & Wilson.** **DIST:** CCo: **CS:** NCI: **DOC:** San Francisco Co.: Howell, J.T. et al. (1958, p. 84): **NOTES:** Probably no more than a casual escape from cultivation.

***Potentilla anglica* Laicharding.** **DIST:** NCo, SCo, ScV, SnFrB: **CS:** NW: **DOC:** Contra Costa Co.: Ertter, B. (1997, pg. 78); Bishop Ranch Regional Open Space southwest of San Ramon, shaded streambed. Aug. 8, 1993, *B. Ertter* and *B. Olson 12198* (UC); **Mendocino Co.:** Smith, G. and C. Wheeler, (1990–1991, pg. 184); **Sacramento Co.:** Wet seep behind house, S end of Blue Oak Flat at summit of American River Bluffs, Folsom Lake State Park, Natoma Unit. Perhaps not persisting. May 21, 1990, *G.F. Hrusa 7930* (CDA); **San Diego Co.:** Poway, Blue Sky Ecological Reserve, Oak Grove area of park, stream edge. Aug. 22, 1995, *M. Hanson s.n.* (UC): **NOTES:** Included in Munz and Keck (1959) but left out of *Jepson Manual* due to lack of sufficient evidence available at the time that this species was truly naturalized in California.

***Potentilla reptans* L.** **DIST:** SnJV: **CS:** TEN: **DOC:** Fresno Co.: Town of Fresno, a lawn weed. June, 1997, *B. Fischer s.n.* (CDA, DAV).

***Prunus laurocerasus* L.** **DIST:** NCo, SCo: **CS:** NW: **DOC:** Humboldt Co.: Arcata, occasional, naturalized in redwood forest behind Humboldt State University, west of Fern Lake, April 12, 2000, *G. Leppig 1291* (CDA, HSC); **Santa Barbara Co.:** upper Alturas Rd., Santa Barbara.

Sept. 30, 1939, *M. Van Rensselaer 1343* (UC): **NOTES:** Escaping from Humboldt State University landscaping.

***Prunus persica* (L.) Batsch.** **DIST:** CaR, SnFrB: **CS:** C: **DOC:** Contra Costa Co.: south base of Mount Diablo, lone tree in Sycamore Canyon, Apr. 25, 1995, *B. Ertter* and *C. Thayer s.n.* (JEPS); **Los Angeles Co.:** Whittier Hills, (Puente Hills, pro parte): Turnbull Canyon nr. mouth. Three trees, escape or persistent from cult.?, no habitations nearby. T2S, R11W Sec. 22. Elev. 505 ft. Apr. 21, 1991, *T. Ross 4499* (CDA, RSA, UC); **Siskiyou Co.:** Mount Shasta, along Everett Memorial Hwy, adventive in chaparral. Elev. 4300 ft. July 4, 1968, *W.B. and V.G. Cooke 39264* (UC).

***Prunus serrulata* Lindl.** **DIST:** SnFrB: **CS:** C: **DOC:** Alameda Co.: Strawberry Canyon firetrail behind UC Berkeley Botanical Garden, several small trees in shady wooded area, Apr. 15, 1999, *B. Ertter 16502* (UC).

***Pyracantha coccinea* M. Roem.** **DIST:** NCoRO, SnFrB: **CS:** TEN: **DOC:** Alameda Co.: Strawberry Canyon, at Poultry Farm Station, 500 ft, Oct. 6, 1934, *C.M. Belshaw 218* (UC). **Sonoma Co.:** Best, C., et al. (1996, pg. 215).

***Pyracantha crenatoserrata* (Hance) Rehder.** **DIST:** CCo, GV, SCo, SnFrB: **CS:** N: **DOC:** Contra Costa Co.: Lime Ridge open space, occasional shrub in grassland of quarry area, May 10, 1998, *B. Ertter 16115* (JEPS); **Sacramento Co.:** Moist disturbed areas in vicinity of Willow Creek parking area, E side Lake Natoma. Common. 38°37'N; 121°02'W. Elev. 75 m. May 2, 1990, *G.F. Hrusa 7802* (CDA); loc. cit. July 26, 1990, *G.F. Hrusa 8155* (CDA); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 147); **Ventura Co.:** Seedlings growing in railroad gravel ballast at Foster Park, Ventura. Aug. 14, 1964, *H.M. Pollard s.n.* (CAS, CDA); Escape from cultivation in brush strip under Ventura River bluff N of and nr Santa Ana Blvd. crossing, Oak View. Oct. 23, 1963, *H.M. Pollard s.n.* (CAS, CDA): **NOTES:** Distinguished by the narrowly obovate leaves to 2 cm wide, often marginally toothed and apically notched. Also observed by Ertter on Albany Hill in Alameda Co. Common as seedlings in urban gardens, lawns. Expected elsewhere.

***Pyracantha crenulata* (D. Don) M. Roem.** **DIST:** NCoRO, SnFrB: **CS:** TEN: **DOC:** Sonoma Co.: Best, C., et al. (1996, pg. 215): **NOTES:** Also observed by Ertter on Albany Hill, Alameda Co.

***Pyrus communis* L.** **DIST:** SCo, ScV, SNE, SnFrB: **CS:** N: **DOC:** Contra Costa Co.: EBMUD land east of Tilden Park, ca. ½ mile southeast of Inspiration Point, grazed grassland near streamlet, single well browsed large shrub. Possibly only persisting from cultivation. May 7, 1993, *B. Ertter* and *C. Thayer 11700* (UC); **Mono Co.:** Spring 0.7 mile S of the mouth of Milner Creek, 0.6 mile N 08° W of Copper Queen Mine, T04S, R33E, Sec. 21, MD. Elev. 5210 ft. Persisting apparently several decades after introduction, compact trees ca. 4 m high in silty moist alluvial soil with *Chrysothamnus*, *Stanleya*, *Robinia*. May 29, 1986, *James D. Morefield* and *Douglas H. McCarty 3718* (RSA, UC); **Orange Co.:** Santa Ana Mountains, 4 mi NE Lake Irvine, Black Star Canyon, Cleveland National Forest, Trabuco District. Oak woodland canyon with riparian woods along the stream. Grassy clearings and chaparral on the canyon slopes. April 18, 1966, *E.W. Lathrop 6176* (RSA); Southern Santa Ana Mountains, San Mateo Canyon Wilderness Area. Western edge of the wilderness in Lucas Canyon along canyon floor from crossing of Lucas Canyon Trail, upstream ¼ mile to spur trail leading to old mining habitations in side canyon, T07S, R06W, Sec. 10, SB. Elev. 1000–1350 ft.



Low shrub, single individual, apparently adventive about old homestead. May 20, 1992, *S. Boyd* and *T. Ross* 7468 (RSA); **Santa Barbara Co.**: Smith, C.F. (1976, pg. 164); **Santa Clara Co.**: Coyote Creek. Mar. 30, 1901, *H.P. Chandler* 911 (UC); **Sonoma Co.**: Pitkin Marsh, near Forestville, eastern branch of the Upper Marsh. At the edge of a thicket, on damp ground. Oct. 26, 1952, *P. Rubtsoff* 1332 (CAS, RSA); W branch upper marsh. Oct. 26, 1952, *Rubtsoff* 1329 (UC); **Ventura Co.**: Matilija Canyon, off-spring of old ranch planting in creek bottom. Oct. 6, 1946, *H.M. Pollard s.n.* (RSA, SBBG); Munz, P.A. (1974, pg. 758); **NOTES**: **Sacramento Co.**: observed as a possible escapes adjacent to orchards approx. one mile S of Freeport.

**Rosa multiflora** Thunb. ex Murray: **DIST**: CaR, CCo, ScV: **CS**: NCI: **DOC**: **Butte Co.**: ca. 5 airmiles southwest of Gridley, south side of Evans Reimer Rd. ca. ¼ mile east of Pennington Road, T17N, R02E, Sec. 07, MD. 70 ft, May 2, 1998, *L. Ahart* 7958 (JEPS); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 148); **Siskiyou Co.**: Mt. Shasta City, sedge meadow at corner of Lake St. and Commercial St. June 9, 2001, *B. Ertter* 17662 (UC); **Shasta Co.**: Squaw Creek Canyon, April 19, 1992, *D.W. Taylor* 12602 (UC). Det. by B. Ertter, 11-2001.

**Rubus ulmifolius** Schott var. *ulmifolius*: **DIST**: CCo, NCoR: **CS**: N: **DOC**: **Napa/Lake Co.**: Highway 29 on north side of Mount St. Helena, roadside at edge of serpentine area, locally common, forming large tangles. Nov. 27, 1997, *B. Ertter* and *L. Constance* 15885 (UC); **NOTES**: Also observed in the Presidio of San Francisco (**San Francisco Co.**) by Ertter.

#### Rubiaceae

**Coprosma repens** A. Rich.: **DIST**: CCo: **CS**: N: **DOC**: **San Francisco Co.**: Howell, J.T. et al. (1958, p. 130); Thomas, H. (1961, p. 323); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 149); **NOTES**: Observed in **Monterey Co.** by Sanders, (10-2000) on seaciffs in Pacific Grove. An escape from cultivation.

#### Salicaceae

**Populus nigra** L. cv. 'Italica': **DIST**: SCo, SNE, NCoR: **CS**: TEN: **DOC**: **Alameda Co.**: Tree NW of Botanical Garden, Strawberry Canyon, Berkeley. July 10, 1943, *B. Rodin* 245 (DAV); **Sonoma Co.**: Best, C., et al. (1996, pg. 221); **Mono Co.**: mouth of Milner Creek, spring 0.7 mi S; 0.6 mi n 83 degrees w of Copper Queen Mine, Owens Valley drainage, White Mountains. Silty moist alluvial soil sloping 3% SW w/*Chrysothamnus*, *Stanleya*, *Salix*, *Rosa*, *Artemisia*. Elev. 5210 ft. T04S, R33E, Sec. 21, MD. May 29, 1986, *James D. Morefield* and *Douglas H. McCarty* 3716e (UC); **Ventura Co.**: Spreading by root-sprouts from parent tree along ditch on Loma Dr. S of Ventura Ave, Ojai Valley, Ventura. Nov. 8, 1967, *H.M. Pollard s.n.* (CAS, CDA); **NOTES**: Perhaps original plants persistent from cultivation, but often spreading aggressively by root sprouts. Best et al. (1996) report that only staminate plants are in cultivation in California.

#### Sarraceniacae

**Sarracenia** aff. *rubra* Walter: **DIST**: NCo: **CS**: N: **DOC**: **Mendocino Co.**: Smith, G. and C. Wheeler (1990–1991, pg. 171); **NOTES**: Intentionally introduced. According to B. Meyers-Rice (DAV) the pitcher plants introduced in this site are represented by hybrid forms. No

clear *S. rubra* has been as yet found, although some individuals may outwardly approach it in appearance.

#### Scrophulariaceae

**Anarrhinum bellidifolium** (L.) Willd.: **DIST**: SnFrB: **CS**: C: **DOC**: **Alameda Co.**: Strawberry Canyon firetrail behind UC Berkeley, 500 m elev., July 18, 1999, *N. Hillyard s.n.* (JEPS); **NOTES**: Determination verified by B. Ertter and M. Wetherwax.

**Limnophila** × *ludoviciana* Thieret: **DIST**: ScV: **CS**: TEN: **DOC**: **Butte Co.**: Rice field at NE corner of Hamilton and Riceton Rds, Rice Experiment Station NW of Biggs. Scattered plants on moist mud betw. experimental rice plots. T19N, R02E, Sec. 35, MD. Elev. ca. 100 ft. Oct. 22, 1998, *Oswald, Ahart, Ertter* 9674 (CDA, CHSC); Rice Experiment Station near Biggs, mud of drained experimental plots, rare. Oct. 22, 1998, *B. Ertter* 16446 with *L. Ahart* and *V. Oswald* (UC), det. by D. Philcox (K), 1998; **Yuba Co.**: Ahart, L. (1981, pgs. 7, 8); In shallow water in open area in a rice field, 2 miles NE of Marysville. Sept. 25, 1977, *L. Ahart s.n.* (CAS, CDA, CHSC) det. by D. Philcox (K), Dec., 1977; **NOTES**: =*Limnophila indica* (L.) Druce × *L. sessiliflora* Blume. Reported by Ahart (1981) as *L. indica*. Examination of both Yuba and Butte Co. material by Philcox (K) indicates our plants are best referred to the hybrid form. Weed of agriculture, subject to elimination via drainage of cultivated rice fields.

**Mazus japonicus** Kuntze: **DIST**: SCo: **CS**: GH/C: **DOC**: **Orange Co.**: Bordier's Nursery, Irvine Boulevard, Santa Ana, spontaneous in locally prepared soil mix. Aug. 9, 1973, *G.D. Barbe* 1694 (CDA, UC).

**Penstemon strictus** Benth.: **DIST**: SNE: **CS**: TEN: **DOC**: **Mono Co.**: Witcher Creek, at crossing of jeep road (Inyo National Forest road 4S54) from Swall Meadows. June 29, 1988, *D.W. Taylor* 9917b (JEPS); **NOTES**: Apparently escaping from nearby rural residential areas of Swall Meadows, either from cultivation or as seeded for 'wildflowers'; common in unmanaged ruderal vegetation of vacant lots in the developed portion of the subdivision. The Witcher Creek location is in an area of natural vegetation removed some 500 m and over a small hill from the most proximal habitations. The occurrence was still present in 1998. Report and data provided by D.W. Taylor.

**Penstemon subglaber** Rydb.: **DIST**: SNE: **CS**: TEN: **DOC**: **Mono Co.**: Mammoth, vacant lot near the Post Office. Aug. 2, 1998, *D.W. Taylor* 16939 (JEPS); **NOTES**: Apparently escaping from nearby areas seeded for 'wildflowers.' The plants reseed in unmanaged, ruderal vegetation in the developed portion of town, but have not yet been seen afar. Report and data provided by D.W. Taylor.

**Scrophularia peregrina** L.: **DIST**: SCo: **CS**: N: **DOC**: **Los Angeles Co.**: Ross, T. and S. Boyd (1996, pg. 436); Claremont, RSABG; SE edge of Indian Hill Mesa, vernal moist clay embankment. Common winter and spring weed in the area. March 24, 1993, *T. Ross* 6819 (CDA, RSA, UC); **NOTES**: Introduced in 1950s during biosystematic study of *Scrophularia*. Robust specimens may mimic *Scrophularia californica*. Native to Mediterranean region.

**Verbascum olympicum** Boiss. non Bunyard: **DIST**: NCoRI: **CS**: NW: **DOC**: **Sonoma Co.**: Common on benches above rocky, dry bed of Leslie Creek from approx. Mark West Ck. confluence to first main tributary from NE. Mixed with *Verbascum thapsus*. July 25, 2000, *G.F. Hrusa* 15690, 15691, 15692 (CDA, and to be distributed); **NOTES**: Readily distinguished from other naturalized *Verbascum* by its dense white-arachnoid pubes-

cence, especially in the inflorescence. Flowers are brighter yellow and larger than in *V. thapsus*. First escaping from ornamental plantings at residence on CAS Pepperwood Preserve in 1976. Population, mixed with *Verbascum thapsus*, is large and apparently increasing. Possible hybrid forms are also scattered at this locality (July 25, 2000, *Hrusa 15693*, CDA).

#### Solanaceae

*Atropa belladonna* L.: **DIST:** CCo, ScV: **CS:** NCI: **DOC:** **Sacramento Co.:** Hampton Rd., Sacramento. Garden weed. Aug. 24, 1999, *Ken and Mary Brown s.n.* (CDA); **San Francisco Co.:** Howell, J.T. et al. (1958, p. 121); Thomas, H. (1961, p. 304).

*Capsicum annuum* L.: **DIST:** SCo: **CS:** NCI: **DOC:** **Ventura Co.:** Spontaneous in fallow field on lower Pierpont Bay, Ventura. Sept. 15, 1959, *H.M. Pollard s.n.* (CDA).

*Cestrum parqui* L'Her.: **DIST:** c SNE, SCo, SnFrB: **CS:** NCI: **DOC:** **Amador Co.:** S side of Jackson on rd to Mokelumne Hill. Aug. 9, 1933, *C.B. Wolf 5206* (UC); **Napa Co.:** Napa City. 1893, *no collector* (UC); **Santa Barbara Co.:** Toro Canyon Creek at Southern Pacific RR crossing, Summerland. Aug. 8, 1961, *H.M. Pollard s.n.* (CDA, SBBG).

*Lycium ferocissimum* Meirs: **DIST:** SCo: **CS:** NCI: **DOC:** **Los Angeles Co.:** shrub 3 m tall, on canal bank in salt marsh, 400 m N of 431 East Culver Blvd, Playa del Rey. T02S, R15W, Sec. 27, SB. Jan. 16, 1979, *T.C. Fuller 20255* (CDA); **NOTES:** Persistent from cultivation?

*Nicotiana × sanderae* Hort. ex Wats.: **DIST:** CCo: **CS:** C: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 121); Thomas, H. (1961, p. 305).

*Nicotiana tabacum* L.: **DIST:** SnFrB, SCo: **CS:** C: **DOC:** **Contra Costa Co.:** 1 volunteer plant at waterfront at E end of building, Golden Gate Fish Co., Point San Pablo, Richmond. Dec. 20, 1966, *R. DeBoer s.n.* (CDA), det. by T.C. Fuller; **San Diego Co.:** Cholla nr. San Diego. Apr. 7, 1885, *Cleveland and Greene s.n.* (UC); **Santa Barbara Co.:** Smith, C.F. (1976, pg. 251).

*Petunia violacea* Lindl.: **DIST:** CCo, SCo: **CS:** NCI: **DOC:** **San Bernardino Co.:** Alta Loma, Hellman and 19th St., roadside. April 2, 1961, *G. Pilone 140* (DAV); **San Luis Obispo Co.:** roadside, no dwelling in vicinity, Perfumo Canyon Rd, 0.9 mi W of junct. with Los Osos Valley Rd., ca. 5 mi SW of San Luis Obispo. July 19, 1962, *T.C. Fuller 9237* (CDA); **Ventura Co.:** Naturalized locally along San Antonio Creek at Royal Oaks Dairy and for some distance downstream, Ojai. Aug. 13, 1966, *H.M. Pollard s.n.* (CDA, SBBG); **NOTES:** An escape from cultivation but extent of true naturalization not known.

*Solanum gayanum* (Remy) Phil. f.: **DIST:** CCo: **CS:** NCI: **DOC:** **San Francisco Co.:** Howell, J.T. et al. (1958, p. 122); Thomas, H. (1961, p. 303); **NOTES:** Escape from cultivation.

*Solanum scabrum* Mill.: **DIST:** ScV, SnJV: **CS:** C: **DOC:** **Butte Co.:** Six volunteer plants, city dump, Sterling City. T24N, R04E, Sec. 28, MD. Sept. 11, 1974, *Sauer and Heinrichs s.n.* (CDA), det. by T.C. Fuller; **Fresno Co.:** Town of Five Points, growing at the Westside Research and Extention Center in mix of seeds of *Solanum nigrum* complex planted in tomato field for herbicide trial. 1999, *Bill Fisher s.n.* (DAV); **Sacramento Co.:** Vigorous growth to 8 dm, vacant lot W side of 1226 D St. Sacramento. Aug. 26, 1988, *G.D. Barbe 4310* (CDA).

*Solanum villosum* Mill.: **DIST:** ScV: **CS:** C: **DOC:**

**Yolo Co.:** Knights Landing, tomato field near wet area. May, 1996, *G. Miyou s.n.* (DAV).

#### Urticaceae

*Boehmeria cylindrica* (L.) Sw.: **DIST:** GV: **CS:** NW: **DOC:** **Sacramento Co.:** *Hrusa, G.F.* (2000, pgs. 138–139); **NOTES:** Observed by *Hrusa* as becoming increasingly common about Snodgrass Slough, Sept. 2001; also observed by *Hrusa* as common in Sutter Slough and Elk Slough (**Yolo Co.**) immed. W of Courtland, Aug. 2002. *Urtica*-like foliage but without stinging hairs, the opposite leaves and inflorescence of sessile, aggregate clusters superficially resemble Lamiaceae. Readily distinguished by the mostly ebracteate inflorescence (although leafy at the apex), scabrous leaves, round stems, absence of a corolla, and unisexual flowers. *Boehmeria cylindrica* may be monoecious or dioecious, but all California material examined to this point is monoecious, with staminate flowers fewer and confined to the uppermost parts of the spike.

*Laportea aestuans* (L.) Chew: **DIST:** SCo: **CS:** GH/C: **DOC:** **San Diego Co.:** Weed in greenhouses. Commercial nursery, Fallbrook. April, 1999, *A. Amador s.n.* (CDA); **NOTES:** Vegetatively similar to *Fatoua villosa* (Thunb.) Nakai, (Moraceae). Seed form unequivocally distinguishes *F. villosa* from the genus *Laportea*.

#### Verbenaceae

*Verbena rigida* Spreng.: **DIST:** CCo, NCoR, ScV, SnFrB: **CS:** NCI: **DOC:** **Contra Costa Co.:** few scattered plants in lawn, Elmwood Rd, El Sobrante. Sept. 3, 1965, *R. DeBoer s.n.* (CDA); **Marin Co.:** Spontaneous in filled ground, San Pedro Rd. at Marin Yacht Club, San Rafael. Filled ground, edge of Yacht Harbor. Sept. 23, 1965, *Gordon True 2652* (CDA); **Sacramento Co.:** spontaneous in sidewalk, 15th and P Sts., Sacramento. Aug. 15, 1961, *R.M. Hawthorne s.n.* (CDA); **Sonoma Co.:** Howell J.T. (1972, pg. 102); **NOTES:** Sometimes treated as *V. venosa* Gillies and Hooker.

*Vitex agnus-castus* L.: **DIST:** SCo, ScV: **CS:** NCI: **DOC:** **Santa Barbara Co.:** naturalized on SPRR tracks at Ortega St., Santa Barbara. June 11, 1968, *P. Okuye s.n.* (CDA); **Yolo Co.:** Creek by apiary, University Farm Campus. Oct. 14, 1932, *H.A. Barthwick s.n.* (DAV).

#### Vitaceae

*Cissus antarctica* Venten.: **DIST:** SCo, SnFrB: **CS:** NCI: **DOC:** **Alameda Co.:** Escaped ornamental, flood channel, Union City. Feb. 2, 1981, *Sweigert s.n.* (CDA); **Los Angeles Co.:** Weed in CalTrans yard betw 710 and 1st. St., East Los Angeles. Oct. 9, 2001, *M. Adams s.n.* (CDA, UCR).

*Vitis aestivalis* Michx.: **DIST:** SCo: **CS:** NCI: **DOC:** **Ventura Co.:** Apparently spontaneous, Valley Rd nr. Santa Ana Blvd., Oak View. June 2, 1972, *H.M. Pollard s.n.* (CAS, CDA).

*Vitis rupestris* Scheele: **DIST:** NCoRO: **CS:** TEN: **DOC:** **Sonoma Co.:** Best, C., et al. (1996, pg. 247); **NOTES:** Winegrape rootstock.

#### Zygophyllaceae

*Peganum harmala* L.: **DIST:** DMoj: **CS:** EXT?: **DOC:** **Kern Co.:** Edwards AFB, roadside ½ mi E of Lancaster Blvd, on Old Hospital Rd. Across from "P" housing section. Single plant. T09N, R10W, Sec. 14, SB. June 29, 1990, *D. Charlton 4453* (CDA); **San Bernardino Co.:** Abandoned 15 acre pasture, Minneola and Elkhorn Rds,

Newberry Springs. T09N, R02E, Sec. 27, SB. July 8, 1988, *J. Hitchcock* s.n. (CDA); 50–60 clumps, 3–5 ft diam. in abandoned pasture, Minneola and Elkhorn Rds, Daggett. T11N, R01E, Sec. 27, SB. July 1, 1988, *J. Hitchcock* s.n. (CDA); Newberry Springs, vicinity of Silver Valley Rd. N of RR tracks nr the airport, in yards of residents and vacant lots. Aug. 23, 1988, *D. Pendleton* s.n. (DAV); **NOTES:** Noxious Weed under eradication by California Dept. of Food and Agriculture.

## ANGIOSPERMS—MONOCOTS

## Alismataceae

*Sagittaria brevirostra* Mackenzie & Bush: **DIST:** CCo: **CS:** NCI: **DOC:** Marin Co: Chileno Valley, the laguna. June 18, 1947, *J.T. Howell* 23261 (UC): **NOTES:** Specimen originally determined as *S. latifolia*; current determination by K. Rataj, 1968, with confirmation by C.B. Hellquist, 1994. Cited in Haynes and Hellquist (2000).

*Sagittaria rigida* Pursh: **DIST:** CaRH, CCo, NCoRI: **CS:** NW: **DOC:** Oswald, V.A. et al. (1998, p. 185): **NOTES:** Introduced to 'improve/enhance' waterfowl habitat?

## Araceae

*Arum palestinum* Boiss.: **DIST:** NCo: **CS:** TEN: **DOC:** Humboldt Co.: Arcata Marsh and Wildlife Sanctuary, Butchers Slough upper salt marsh. May 8, 1998, *G. Lepig* 755 (CDA, HSC); Humboldt Bay, Woodley Island near hunting cabin, moist *Juncus* meadow. UTM Zone 10 4518N 4020E. July 14, 1976, *Peter Sorenson* s.n. (HSC): **NOTES:** This species, although locally present in small numbers is long-lived and thus highly persistent. Arcata Marsh population under eradication by City of Arcata.

*Dracunculus vulgaris* Schott: **DIST:** SCo, SnFrB: **CS:** N: **DOC:** Alameda Co.: ca. halfway up Claremont Canyon in Oakland Hills, locally established colony on steep roadfill. June 16, 1995, *B. Ertter* and *L. Constance* 14258 (UC); loc. cit. June 7, 1992, *B. Ertter* 11082 (UC); **Santa Barbara Co.:** Santa Barbara, growing in lot probably once under cultivation. May 17, 1948, *R.S. Beal, Jr.* s.n. (UC): **NOTES:** Claremont Canyon colony still present as of April 1990, possibly expanding.

*Pinellia ternata* (Thunberg) Makino: **DIST:** SnFrB: **CS:** NCI: **DOC:** San Francisco Co.: Golden Gate Park, "accidentally introduced". May, 1935, *E. Walther* s.n. (UC): **NOTES:** Determined by S.A. Thompson, 1994; original determination as *P. tripartita* (Blume) Schott.

## Cyperaceae

*Bulbostylis barbata* Kunth: **DIST:** CCo: **CS:** GH/C: **DOC:** Santa Cruz Co: Weed growing in commercial greenhouses, Watsonville. Probably originating from Sri Lanka. May 14, 1998, *T. Watson* s.n. (CDA).

*Cyperus flavescens* L.: **DIST:** ScV: **CS:** NW: **DOC:** Butte Co.: damp sand, E side Sac. R., NW Parrott Landing, 1 mi SE Ord Ferry, 12 mi SE Chico. Aug. 13, 1999, *Lowell Ahart* and *V. Oswald* 8143 (CDA, CHSC), det. by V. Oswald, 10-99; loc. cit. Oct. 28, 1999, *L. Ahart* 8303 (CHSC); Arch Rock tunnel, Feather River Hwy, Elev. 500 m. Sept. 6, 1981, *L. Ahart* 3123 (CHSC, DAV); Peter Ahart Ranch, 1 mi N and 2 $\frac{3}{4}$  mi E of Honcut. July 19, 1975, *L. Ahart* 901 (CHSC); loc. cit. Aug. 21, 1975, *L. Ahart* 957 (CHSC); loc. cit. Sept. 4, 1987, *L. Ahart* 5877 (CHSC); loc. cit. Aug. 19, 1995, *L. Ahart* 7618 (CHSC, JEPS); wet sand on N. Fk. Feather River nr Poe Powerhouse, riparian woodland, elev. 890 ft. Aug. 30, 1987, *L.*

*Ahart* 5865 (CHSC); wet sand on margins of small pond in Oroville Wildlife Area. Common. Elev. 140 ft. Aug. 23, 2000, *L. Ahart* 8664 (CHSC); moist gravel bar along Sacramento R. 0.25 mi downstream from Murphy's Slough. Riparian woodland. July 31, 1983, *V. Oswald* 941 (CHSC); Feenstra's Riverview Orchard W end of Cana Hwy between S half Cana Lake (on Dicus Slough) and Sacramento River. Uncommon. Wet gravel near shallow pools on large gravel bar along river. Portion of Rancho Bosquejo, elev. 160 ft. T23N, R02W, MD. Aug. 13, 1987, *V. Oswald* 3215 (CHSC); **Tehama Co.:** Hog Lake Plateau along Hwy. 36 NE of Red Bluff, T28N, R03W, Sec. 14, MD, elev. 430 ft, moist soil along Paynes Creek ca. 1 mi upstream from the old bridge site. Sept. 4, 1996, *V. Oswald* and *L. Ahart* 8270 (CHSC), det. L. Janeway; **Yuba Co.:** Wet soil in irrigated pasture on Eugene Ahart Ranch in Marysville, elev. 100 ft. Sept. 11, 1975, *L. Ahart* s.n. (CHSC), det. V. Oswald; shallow water on disturbed rocky soil, S side Scott Forbes Rd, 0.25 mi E of intersection Scott Forbes Rd and Peoria Rd. E of Gray Dr., E of Browns Valley. Uncommon, el. 300 ft. Aug. 13, 1997, *L. Ahart* 7865 (CHSC), det. V. Oswald: **NOTES:** Additional collections from some of these same localities are at CHSC, the earliest from 1961.

*Cyperus flavicomus* Michx.: **DIST:** ScV, SNF: **CS:** N: **DOC:** Butte Co.: University of California Biggs Rice Research Station, near the corner of Riceton and Hamilton Roads, in rice field, Aug. 30, 2000, *DiTomaso* s.n. (DAV); Edge of Middle Honcut Road, about  $\frac{3}{4}$  mile E of Hwy 70, ca. 12 mi S of Oroville, common, valley grassland, *L. Ahart* 4810 (CHSC); 8 mi NE of Butte City, ditch bank. Oct. 15, 1946, *J.E. Chittin* and *C. Ferrell* s.n. (UC); **Tulare Co.:** 3 mi below Three Rivers. Sept. 25, 1920, *L. Abrams* 7715 (CAS): **NOTES:** Determination of *DiTomaso* s.n. by G.C. Tucker. The Ahart and Abrams specimens were originally determined as *Cyperus albomarginatus* Mart. & Schrad., a synonym of *C. flavicomus*; however, the original determinations as *C. albomarginatus* have not yet been confirmed.

*Cyperus gracilis* R. Br.: **DIST:** SCo: **CS:** NCI: **DOC:** Los Angeles Co: volunteer in residential garden, Santa Monica. Aug. 20, 1983, *Tom Yutani* s.n. (CDA).

*Cyperus iria* L.: **DIST:** SCo, ScV: **CS:** TEN: **DOC:** Santa Barbara Co.: Germinating in coco fiber from Sri Lanka. Commercial greenhouse in Carpinteria. Grown to maturity in CDA greenhouse, Sacramento. Oct. 14, 1998, *T. Watson* s.n. (CDA); **Yuba Co.:** Dry to damp soil, disturbed area S side Woodruff Lane, just W Kimball Lane, 5 mi NE Marysville. Elev. 80 ft. Sept. 5, 1999, *L. Ahart* 8197 (CDA, CHSC).

*Cyperus owanii* Boeck: **DIST:** CCo, SCo: **CS:** NCI: **DOC:** Los Angeles Co.: Spontaneous, UCLA Bot. Garden, Westwood. April 19, 1972, *T.C. Fuller* 19941 (CDA); **San Diego Co.:** Barranca, Balboa Park, San Diego. April 22, 1969, *T.C. Fuller* 18244 (CDA); loc. cit. Oct. 21, 1969, *T.C. Fuller* 19012 (CDA, DAV); **San Francisco Co.:** Golden Gate Park, California Academy of Sciences, San Francisco. Oct. 18, 1967, *T.C. Fuller* 16748; loc. cit. Nov. 21, 1968, *T.C. Fuller* 18013 (CDA); **Santa Barbara Co.:** Smith, C.F. (1976, pg. 94): **NOTES:** Only known occurrences in North America N of Mexico.

*Cyperus papyrus* L.: **DIST:** SCo: **CS:** NCI: **DOC:** San Diego Co.: Beauchamp, R.M., (1986, pg. 48).

*Fimbristylis autumnalis* (L.) Roem. & Schult.: **DIST:** ScV: **CS:** NW: **DOC:** Butte Co.: Disturbed area E side Sacramento River NW Parrott Landing, 1 mi SE Ord Ferry, 12 mi SW Chico. Riparian woodland. Aug. 13, 1999, *L. Ahart* 8145 and *V. Oswald* (CDA, CHSC).

*Scirpus cyperinus* (L.) Kunth: **DIST:** c SNF: **CS:** NW: **DOC:** **Mariposa Co.:** Moist banks and alluvial flats, Merced River near mouth Yosemite Creek, Yosemite Valley. Aug. 13, 1976, *J.T. Howell 52233* (CAS, CDA); loc. cit. Sept. 28, 1978, *G.D. Barbe 2447, 2444* (CDA, CHSC): **NOTES:** Determination confirmed by L. Janeway (CHSC) 2-2000.

*Scirpus prolifer* Rottb.: **DIST:** SCo: **CS:** NCI: **DOC:** **San Diego Co.:** Persisting in sandy soil of lathhouse, 19 km NW of Fallbrook. Nov. 14, 1978, *G.D. Barbe 2472* (CDA, DAV).

#### Eriocaulaceae

*Eriocaulon cinereum* R. Br.: **DIST:** SnJV: **CS:** EXT: **DOC:** **Stanislaus Co.:** Krause rice fields, Modesto. Sept. 18, 1947, *B.G. Markos s.n.* (CDA): **NOTES:** Extirpation likely as rice fields are no longer maintained in the Modesto region. Cited from California in *Flora North America* (Kral 2000).

#### Hydrocharitaceae

*Limnobiium laevigatum* (Humb. & Bonpl. ex Willd.) Heine: **DIST:** SCo, SnFrB: **CS:** NW: **DOC:** **Alameda Co.:** Jordan Pond in Garin Park; East Bay Regional Park District, Hayward. Floating and rooted in bottom mud. Oct. 31, 1996, Sept. 21, 1998, Oct. 22, 1998, *R. Eaton s.n.* (CDA); Garin Regional Park east of Hayward, silted-in pond below Jordan Pond, well-established colony both floating and stranded. Sept. 4, 1998, *B. Ertter 16408* (UC); rimming Jordan pond, some in bloom, Oct. 24, 1998, *B. Ertter 16458* (UC); **Riverside Co.:** Covering  $\frac{1}{4}$  acre of outdoor pond at Desert Lawn Cemetery, Desert Lawn Dr., Calimesa. T02S, R01W, Sec. 31. SB. Aug. 23, 1999, *J. Chandler s.n.* (CDA): **NOTES:** **Santa Cruz Co.:** in a backwater of the San Lorenzo River. Voucher specimen not yet received, but scrap material confirmed by B. Ertter in fall 2000. Not relocated in spring 2001. Floating or stranded rosettes spreading by stolons; leaves  $\pm$  round, 1–3.5 cm across, sessile to long-pediceled, convexly spongy on underside. Sometimes treated as *L. spongia* subsp. *laevigatum* (Humb. & Bonpl. ex Willd.) Lowden. As observed by Ertter, eradication effort in Jordan Pond by East Bay Regional Parks District (EBRPD) has not yet succeeded in eliminating the *Limnobiium*, but has concurrently severely impacted the originally diverse aquatic flora, underscoring just one of the major problems inherent in the control of aquatic pests. This plant is currently prohibited from being sold commercially in California; however, as in the case of *Salvinia molesta*, it remains for sale by aquatic plant nurseries and dealers. The closely related *Limnobiium spongia* (Bosc) Steud. (*sensu stricto*) is currently offered for mail-order sale by midwest nurseries and is thus eventually expected to escape in California. Both taxa are a threat to California wild wetlands, irrigation ditches, canals, sloughs, farm ponds or private lakes, and if either should become established in navigable waterways they are especially likely to spread rapidly and widely. The two established and reproducing colonies described above are in non-navigable waters. It should also be noted that any number of aquatic taxa sold unlabeled in California nurseries could be *Limnobiium* or other unidentified taxa which could display the same degree of aggressiveness as does *Limnobiium* should they be introduced into aquatic habitats where there are no natural controls.

#### Iridaceae

*Iris foetidissima* L.: **DIST:** NCoRO, SnFrB: **CS:** N: **DOC:** **Alameda Co.:** well established along a stretch of the Golden Spike Trail in Redwood Regional Park, Oakland Hills. Oct. 15, 2000, *Ertter 17542* (UC); **Contra Costa Co.:** Sibley Volcanic Preserve in Oakland Hills, single clump in understory of oak-pine forest behind interpretive center. May 20, 2000, *B. Ertter 17025* (UC); **Sonoma Co.:** Best, C., et al. (1996, pg. 261): **NOTES:** Spreads readily in garden situations. Seeds with red arils indicate a high potential for bird dispersal into wildlands.

*Iris germanica* L.: **DIST:** NCoRO, SnFrB: **CS:** TEN: **DOC:** **Santa Barbara Co.:** Munz, P.A. (1974, pg. 907); **Sonoma Co.:** Best, C., et al. (1996, pg. 261): **NOTES:** Seen often about old habitations and sometimes persistent long after signs of human infestation have disappeared. Citations here both imply local naturalization. Also observed as a casual in **Alameda** and **Contra Costa Cos.**

*Iris orientalis* L.: **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Smith, C.F. (1976, pg. 106).

*Ixia polystachya* L.: **DIST:** NCo: **CS:** NCI: **DOC:** **Mendocino Co.:** persisting in scattered locations among the headstones of Evergreen Cemetery, Hwy 1 at Mountain View Rd, 1 mi S of Manchester. T13N, R17W, Sec. 06, MD. May 27, 1982, *G.D. Barbe 3628* (CAS, CDA): **NOTES:** dupl. det. by J.M. Mullin, 1983 (BM).

*Ixia speciosa* Andrews: **DIST:** NCo: **CS:** NCI: **DOC:** **Mendocino Co.:** Smith, G. and C. Wheeler (1990–1991, pg. 113).

*Moraea collina* Thunb.: **DIST:** CCo: **CS:** N: **DOC:** **Santa Cruz Co.:** remnant native coastal prairie site on marine terrace lying between Rodeo Gulch and Hidden Valley Road, ca. 75 meters SSE of pole 14/117 of the PG and E Paul Sweet-Green Valley 115 kv double-wood pole transmission line (site is 1.5 air mi NNE of Dominican Hospital); elev. 370 ft, grassland on edge of thickets of *Quercus agrifolia*. May 2, 2000, *D.W. Taylor 17446* (JEPS): **NOTES:** Naturalization localized at present. Goldblatt (1998) treats this as *Moraea collina* Thunb., not as *Homeria* (Thunb.) Salisb. which is the name in use by the horticultural trade and by Australian authors. The entire genus *Homeria* is on the Federal Noxious Weed Act quarantine list (see Federal Register, May 25, 2000, p. 33741–33743), and is thus illegally sold, although commonly available in California nurseries. Native to South Africa. Related species are aggressive invaders of pastures in New Zealand, Australia. All *Homeria* spp. are toxic to livestock.

*Moraea polystachya* Ker Gawl.: **DIST:** SCo: **CS:** NCI: **DOC:** **Santa Barbara Co.:** Plants abundantly naturalized on roadside, N side of Cabrillo Blvd., SW corner of Bird Lagoon, Montecito. T04N, R27W, Sec. 24, SB. Dec. 11, 1968, *T.C. Fuller 18041*; loc. cit. Mar. 23, 1971, *T.C. Fuller 19820* (CDA).

#### Juncaceae

*Juncus nodatus* Cov.: **DIST:** SnFrB: **CS:** N: **DOC:** **Alameda Co.:** UC-Berkeley Botanical Garden, edge of path near vernal pool section. July 16, 1998, *H. Forbes s.n.* (UC): **NOTES:** Well-established local colony, not derived from cultivated material. Determination by B. Ertter.

#### Liliaceae (*sensu lato*)

*Agapanthus praecox* Willd.: **DIST:** CCo: **CS:** NCI: **DOC:** **San Mateo Co.:** McClintock, E., et al. (1990, pg. 167): **NOTES:** Clearly originating as a garden escape.

**Allium cepa L.**: **DIST**: NCoRO: **CS**: NCI: **DOC**: **Sonoma Co.**: Best, C., et al. (1996, pg. 269): **NOTES**: A local garden escape in 1963, probably not persistent.

**Allium sativum L.**: **DIST**: NCoR: **CS**: C: **DOC**: **Sonoma Co.**: Best, C., et al. (1996, pg. 269): **NOTES**: A local garden escape.

**Amaryllis belladonna L.**: **DIST**: CCo, SCo, SnFrB, SnBr: **CS**: TEN: **DOC**: **Contra Costa Co.**: observed by Ertter near Donner Cabin, Mount Diablo State Park [voucher prepared but lost]; observed elsewhere in San Francisco Bay Area.; **Los Angeles Co.**: Malibu, upslope from Winter Canyon, near Pepperdine Univ., N of Pacific Coast Hwy, E of Malibu Cyn Rd., SW of Malibu Civic Center Way, elev. ca. 300 ft, 34°02'N; 118°42'W, T01S, R17W, Sec. 31, SB. Mar. 15, 1995, S. White 2585 (UCR); **Monterey Co.**: Yadon, V. (1995); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 167); **Sonoma Co.**: Sea Ranch, just ESE of Leeward Rd. entrance along State Hwy. 1. Aug. 13, 1975, M. Hektner 220 (DAV), voucher for Wasmann J. Biol. 35(1):26–53: **NOTES**: Also observed by Sanders apparently naturalized near Yucaipa, **San Bernardino Co.** Cultivated widely. Often long-persistent from cultivation and known from numerous homestead sites in northern and southern California.

**Chlorophytum capense (L.) Druce**: **DIST**: CCo: **CS**: C: **DOC**: **San Francisco Co.**: Howell, J.T. et al. (1958, p.53); Thomas, H. (1961, p. 117): **NOTES**: A garden escape.

**Hyacinthus orientalis L.**: **DIST**: CCo: **CS**: C: **DOC**: **San Francisco Co.**: Howell, J.T. et al. (1958, p. 53); Thomas, H. (1961, p. 117): **NOTES**: A garden escape.

**Kniphofia uvaria (L.) Hooker** [or hybrid derivative]: **DIST**: CCo, NCo, SCo, SnFrB: **CS**: NW: **DOC**: **Alameda Co.**: North foot of Albany Hill (eliminated by subsequent roadwork). May 25, 1992, B. Ertter 11070 (UC); **Contra Costa Co.**: Miller Knox Regional Park, open hillside south of watertank, single large patch, expanding. Mar. 21, 1999, B. Ertter 16487 (UC); **Humboldt Co.**: Arcata Marsh and Wildlife Sanctuary, dike at Klopp Lake, on disturbed fill on Humboldt Bay. April 9, 2000, G. Leppig 1287 (CDA, HSC); **Mendocino Co.**: Smith, G. and C. Wheeler (1990–1991, pg. 107); Hwy. 1 at Navarro Rd, 7.5 miles S of Elk. Roadside pastures. Common. July 9, 2000, G. Leppig 1459 (CDA, HSC); Sinkyone Wilderness State Park, mouth of Jackass Creek at the end of Wheeler Rd. Old home site on the S side of Cyn. T23N, R19W, Sec. 01, MD. May 28, 1987, F. Bowcutt 1011 (DAV); **San Francisco Co.**: Howell, J.T. et al. (1958, pg. 53); **San Mateo Co.**: McClintock, E., et al. (1990, pg. 168); **Santa Barbara Co.**: upper east fork of Cold Spring Canyon above Montecito. Jan. 21, 1967, H.M. Pollard s.n. (SBBG, UCR); **Sonoma Co.**: Best, C., et al. (1996, pg. 275): **NOTES**: Expected elsewhere. Can be long persistent from cultivation as at Fort Hunter Liggett (Monterey Co.) where it is found about old homesteads without any indication of spontaneity. Other 'populations' may originate via garden trash, but many locations are obviously spontaneous. Observed in coastal meadows and on roadsides, where occasional to common in **Monterey Co.** but not yet vouchered. Also observed in locations other than the records above in Sonoma, Mendocino and Humboldt Cos.

**Leucocjum aestivum L.**: **DIST**: CCo: **CS**: NCI: **DOC**: **San Luis Obispo Co.**: Keil, D.J., et al. (1985, pg. 222).

**Narcissus pseudonarcissus L.**: **DIST**: NCo, SnFrB: **CS**: NW: **DOC**: **Contra Costa Co.**: Mount Diablo State Park, Donner Cabin site, persisting colony. Feb. 16, 1997, B. Ertter 15451 (JEPS); northwest end of Wildcat Canyon Park, occasional clumps among brush-grassland mosaic.

Mar. 7, 1999, B. Ertter and L. Fujii 16485 (UC); Molate Beach Park, coastal prairie. April 7, 1996, B. Ertter 14581 (UC); **Humboldt Co.**: Fickle Hill Road, abundant in open areas. T06N, R01E, Sec. 27, H. Mar. 9, 1963, J.C. Reppas 18 (HSC); Old Arcata Road at Jacoby Creek Rd., common along roadsides, T05N, R01E, Sec. 16, H. Apr. 8, 1965, N.D. Dennis 15 (HSC); North Bank Rd., 4 mi N of Arcata, escaped from cultivation, R01E, T06N, Sec. 09, H. Apr. 14, 1965, J. L. Baker 1965 (HSC): **NOTES**: A diversity of hybrid cultivars are also sporadically encountered (e.g., Molate Beach Park, **Contra Costa Co.**) These may be persistent from cultivation, the remnants of garden trash, or spontaneous.

**Narcissus tazetta L.**: **DIST**: NCo, SnFrB: **CS**: NW: **DOC**: **Contra Costa Co.**: Mount Diablo State Park, Back Canyon Road at cross road above Donner Canyon trailhead, seepage area in grassland, well established spreading colony. Jan. 25, 1998, B. Ertter and A. Dennis 15910 (JEPS); **Humboldt Co.**: Patrick's Point State Park, near Ceremonial Rock. 21 July 1986, E. Mackey s.n. (HSC).

**Ornithogalum umbellatum L.**: **DIST**: CCo, NCoRI: **CS**: GH/C: **DOC**: **Lake Co.**: Upper Lake, along Mendenhall Rd, off Hwy 20, in walnut orchard. Apr. 4, 2000, R. Elkins s.n. (DAV); **Santa Cruz Co.**: Garden weed, Riverside Dr., Watsonville. Apr. 12, 1971, D.H. Shaw s.n. (CDA).

**Pancratium maritimum L.**: **DIST**: SCo: **CS**: N: **DOC**: **Los Angeles Co.**: El Segundo Dunes, immediately west of L.A. International Airport and Pershing Dr., E of Vista Del Mar Blvd., nr. 33°56'N; 118°26'W, coastal dunes formerly largely occupied by residential neighborhoods, the houses removed ca. 15 years ago. Assoc. with *Croton californicus*, *Abronia umbellata*, *Camissonia cheiranthifolia* and various persisting ornamentals. Forming vegetative clumps in sand; also some reproduction by seed. July 22, 1987, A.C. Sanders 7156 (RSA, SBBG, UCR): **NOTES**: An escaping ornamental; native to beaches in southern Europe. Reported also from **Ventura Co.** at Mugu Lagoon and San Buenaventura State Beach, but no specimens yet available for confirmation.

**Tulipa clusiana DC. in Redoute**: **DIST**: SCo: **CS**: TEN: **DOC**: **Riverside Co.**: City of Riverside, east edge near Moreno Valley, spontaneous at the site of the former Desert Nursery, N of Hwy 60, E of Day Street, unknown origin, possibly accidentally introduced with other plant material, now reproducing and increasing in one area with no care or watering. Mar. 23, 1994, A. Miller 94-1 (UCR): **NOTES**: At almost the same time as this collection, this species was reported to Sanders as a lawn weed in Riverside, but no voucher materialized. This plant is apparently a common weed in the Mediterranean basin. It is quite showy and might get moved around intentionally as an ornamental.

#### Poaceae

**Acrachne racemosa (Roem. & Schult.) Ohwi**: **DIST**: SCo: **CS**: TEN: **DOC**: **Riverside Co.**: Sanders, A.C., (1996, pg. 524).

**Aira caryophyllea L. var. cupaniana (Guss.) Fiori**: **DIST**: SnFrB: **CS**: NCI: **DOC**: **Contra Costa Co.**: Mount Diablo State Park, Wall Point Road, prescribed burn. May 28, 1995, M.L. Bowerman s.n. (JEPS), verified by J. Wipff, 1998: **NOTES**: =*Aira cupaniana* Guss. Not relocated in 1998–99.

**Amphibromus neesii Steud.**: **DIST**: ScV: **CS**: NW: **DOC**: **Sacramento Co.**: grown to maturity in greenhouse from plant dug out of large colony in vernal pool at corner

of Sunrise and Keifer Aves., SE of Sacramento. July 28, 2000. *G.F. Hrusa s.n.* (CDA). **NOTES:** Although known from only a single site, this species is of particular interest because of its ability to invade and survive in vernal pools. Native to and sometimes listed in the Australian literature under the synonym *Amphibromus nervosus* (R. Br.) Druce. First seen in this site in 1990 by J. Glazner of North Fork Associates, Auburn, CA (personal communication to Hrusa). *Amphibromus neesii* forms cleistogamous seeds; these first noted and identified at the California Dept of Food and Agriculture Analysis and Identification (now Plant Pest Diagnostics) Branch Seed Laboratory in 1967 as a contaminant in *Trifolium subterraneum* seed imported from Australia.

**Aristida dichotoma Michx.** **DIST:** n SNF: **CS:** NW: **DOC:** **Butte Co.:** Dry bare granite soil, Big Bald Rock. Uncommon, inconspicuous. Yellow pine forest, elev. 3260 ft. Aug. 5, 2000, *L. Ahart 8623 and V. Oswald* (CDA, CHSC); Dry bare granite soil above seeps on bare granite. N side Bean Ck. Rd., ~ ¼ mi. SE Little Bald Rock and 1¼ mile NE Big Bald Rock, 4 air miles NE Madrone Lake and 13 mi NE of Oroville. Uncommon. Yellow pine forest, elev. 3500 ft. T21N R06E, Sec. 29, MD. Aug. 5, 2000, *L. Ahart 8624 and V. Oswald* (CDA, CHSC). **NOTES:** Determinations by K. Allred (NMCR).

**Chloris truncata R. Br.** **DIST:** DSon, SCo, SnJV: **CS:** N: **DOC:** **Imperial Co.:** Weed in alfalfa, 5 mi S of El Centro and 3.5 mi. SW of Heber. T16S R13E, Secs. 35, 36. Aug. 8, 2000, *J. Johnson s.n.* (CDA, DAV); **Merced Co.:** Almond orchard at corner of Vista Ave and Hwy. 99 S, N of Chowchilla. July 19, 1999, *J. DiTomaso s.n.* (CDA, DAV); **Riverside Co.:** Sanders, A.C., (1996, pg. 526; 1999, pg. 113); Weedy in hybrid bermudagrass turf, turfgrass nursery, Leon Rd. Winchester. Nov. 9, 1978, *E. Storm s.n.* (CDA), det. by G.F. Hrusa, Oct., 1999.

**Echinochloa crusgalli subsp. spiralis** (Vasing.) Tzvel-ev: **DIST:** ScV, SnGB: **CS:** N: **DOC:** **Butte Co.:** Afton Rd. nr. Biggs. Aug. 23, 1947, *M.K. Bellue s.n.* (CDA); In milo field. Sept. 16, 1958, *J. Harroun s.n.* (CDA); **Los Angeles Co.:** San Gabriel Mtns., Angeles National Forest: Little Rock Reservoir, dry sunny sandy flat toward upper end. Sept. 6, 1966, *L.C. Wheeler 8873* (CDA, RSA); **Sacramento Co.** sine loc. July, 1943, *Bellue s.n.* (CDA). **NOTES:** First report of this variety for North America. Expected widely. Determinations by S.L. Mosyakin (KW), March 26, 2001.

**Echinochloa esculenta** (A. Br.) H. Scholz: **DIST:** NCo, SCoRI, SnJV: **CS:** NCI: **DOC:** **Del Norte Co.:** Abundant along a slough, Reservation Ranch, Smith River. Oct. 2, 1968, *E.J. Garrett s.n.* (CDA); **Monterey Co.:** near Chualar. Sept. 1938, *McElrath s.n.* (CDA); **Fresno Co.:** near Fresno. Sept., 1938, *McElrath s.n.* (CDA). **NOTES:** Determinations by S.L. Mosyakin (KW), March 26, 2001. *Echinochloa frumentacea* Link (*E. crusgalli* var. *frumentacea* (Link) Trimen) has been consistently misapplied to this plant in California. It is probably most often an escape from cultivation, although populations may be locally persistent.

**Ehrharta longiflora Sm.** **DIST:** SCo: **CS:** NW: **DOC:** **San Diego Co.:** Simpson, M.G., et al. (1996, pg. 79). **NOTES:** Known only from a single location.

**Eragrostis curvula** (Schr.) Nees var. *conferta* Nees: **DIST:** SCo: **CS:** N: **DOC:** **Riverside Co.:** Sanders, A.C. (1996, pg. 527).

**Eremochloa ciliaris** (L.) Merr.: **DIST:** CCo: **CS:** EXT: **DOC:** **San Francisco Co.:** Thurber, G. in S. Watson, (1880, pg. 261–2). **NOTES:** Original report as *Ischaemum leersioides* Munro (specimen at CAS). Citation in Howell,

J.T. et al. (1958), is based on the above report. Extirpation is assumed although there has been no thorough investigation of its presence or absence.

**Gaudinia fragilis** (L.) P. Beauv.: **DIST:** NCoRO: **CS:** NW: **DOC:** **Sonoma Co.:** Daniel, T. and C. Best (1992, pp. 309–310); Best, C., et al. (1996, pg. 300). **NOTES:** Reported location highly localized, should be sought elsewhere in the region.

**Glyceria fluitans** (L.) R. Br.: **DIST:** CaRH, NCo, NCoRI: **CS:** NW: **DOC:** **Del Norte Co.:** Veneer Mill pond, Redwood NP. June 5, 1995, *G. Leppig 242* (CDA, HSC); **Humboldt Co.:** Arcata Bottom, wet slough. July 20, 1933, *J. T. Tracy 12801* (HSC, RSA); Stone Lagoon moist field. Aug. 3, 1924, *J. T. Tracy 6749* (RSA); Arcata, Alder Grove Pond, on edge of pond. June 4, 1995, *G. Leppig 242* (CDA, HSC); loc. cit. May 25, 1998, *G. and S. Leppig and K. Neander 791* (CDA, HSC); loc. cit. April 24, 1999, *G. and S. Leppig 1125* (CDA, HSC); **Lake Co.:** Kelseyville, swampy places. June 8, 1924, *J.W. Blankinship s.n.* (RSA); **Shasta Co.:** Cassel. June 24, 1930, *M. Kjilsberg s.n.* (DAV). **NOTES:** According to G. Leppig (HSC), this may be an overlooked native.

**Hordeum vulgare** L. [*sensu lato*. Including material referable to var. *trifurcatum* (Schlecht.) Alef.]: **DIST:** CAF: **CS:** C: **DOC:** **Alpine Co.:** W Fk. Carson River, ca. 1 mi W from Woodfords along Crystal Springs Rd. June 22, 1974, *D.W. Taylor 3911* (UC); **Los Angeles Co.:** San Clemente Island, widely scattered over mesa summit and S slopes. May, 1936, *N. Murbarger 174* (UC); **Marin Co.:** nr. Inverness. June 3, 1945, *J.T. Howell 20918* (UC); **Mariposa Co.:** valley floor, Yosemite Valley, Yosemite Natl. Park. Apr. 1, 1934, *P.S. Bartholomew s.n.* (UC); **Mendocino Co.:** nr. Ukiah, volunteer in oat-field. May 25, 1899, *J. Burt Davy and W.C. Blasdale 5059* [awned] (UC); May 25, 1899, *J. Burt Davy 5058* [awned] (UC); **Sacramento Co.:** Volunteering in residential garden. Mar. 29, 1979, *K. Miller s.n.* (CDA); **San Diego Co.:** Simpson, M.G. et al. (1996, pg. 80); **San Luis Obispo Co.:** ROW along Hwy 46 approx. 4 mi E Paso Robles. Weed on roadside, solitary. Elev. 200 m. 35°39'N; 120°26'W. Apr. 4, 1992, *G.F. Hrusa 10345* (CDA); Cuyama Valley, weed at edge of barley field, immed. W of int. Hwy 33 and Hwy 166. Penetrating into planted field along edges. Elev. 650 m. 34°55'N; 119°33'W. Apr. 26, 1998, *G.F. Hrusa 14276* (CDA); **Siskiyou Co.:** Volunteer; subsaline flat and roadside, betw. Old Highway 99 and RR at Trutman Lane, 3.2 km S of Grenada. Elev. 800m. T44N, R06W, Sec. 34, MD. Apr. 28, 1980, *G.D. Barbe 2589* (CDA); **Ventura Co.:** San Nicolas Island, N edge of mesa, E end of old landfill, E of Living Compound. Apparently used for erosion control on inactive landfill site. Apr. 1, 1992, *S. Junak SN-789* (JEPS, SBBG). **NOTES:** Although sporadic occurrences are well-documented, these were all determined to be casuals and accordingly the species was not included in *The Jepson Manual*. This species is also commonly used for roadcut erosion control and it may be difficult to determine if a local site or population is established or recently planted. Records listed above are representative; the species can be expected in every California county. Numerous unvouchered records are on file at CDA (based on specimens submitted but not retained); observed as common on road cutbanks throughout northern California, especially so along that part of the Interstate 5 corridor. *Hordeum vulgare* var. *trifurcatum* is a hooded form, reported as a roadside weed almost as often as the typical variety, although probably due to its visible distinctiveness and not frequency. Annotations at UC by N. Jacobsen (1980) do not recognize var. *trifurcatum*.



**Leptochloa dubia (Kunth) Nees:** DIST: CaRF/n SNF: CS: N: DOC: **Butte Co.:** west side of Hwy 70 ca. 1½ miles north of bridge across the West Branch of Lake Oroville, just north Rich Gulch Road, T22N, R04E, Sec 09, elev. 1300 ft. Common on dry rocky disturbed soil. Sept. 6, 1997, L. Ahart 7894 (CHSC, JEPS).

**Nassella tenuissima (Trin.) Barkworth:** DIST: CCo: CS: C: DOC: **Contra Costa Co.:** Creekside Park, El Cerrito, overflow basin for Cerrito Creek, single vigorous plant. July, 2000, B. Ertter s.n. (UC): **NOTES:** Also readily establishing in sidewalk cracks adjacent to cultivated plants in gardens throughout Berkeley, this species has a high potential for spread into natural areas. A popular horticultural species whose weedy behavior should be carefully monitored.

**Panicum maximum Jacq.:** DIST: SCo: CS: GH/C: DOC: **Riverside Co.:** Sanders, A.C. (1996, pg. 529).

**Panicum repens L.:** DIST: SnFrB: CS: NCI: DOC: **Alameda Co.:** abundant weed of ornamental shrubs, climbing to 3 ft high in some shrubs, Oxford Tract, U.C. campus, NE corner of Walnut St. and Hears Ave., Berkeley. T01S, R04W, Sec. 02, MD. Nov. 21, 1968, T.C. Fuller 18011 (CDA): **NOTES:** Rhizomatous perennial introduced into California from Florida in *Melaleuca* stock.

**Panicum rigidulum Bosc ex Nees var. rigidulum:** DIST: ScV, n SnJV: CS: NCI: DOC: **Butte Co.:** Bank of Feather River, Oroville, elev. 175 ft. Sept. 22, 1961, J.T. Howell 36714 (CAS, CDA), original det. as *P. agrostoides* Spreng.; **Sacramento Co.:** 1 mi S of Fair Oaks along American River. Growing in sandy gravel of dry flood banks along river. Oct. 31, 1961, B. Crampton 6072 (AHUC); loc. cit. Oct. 16, 1953, B. Crampton 1706 (AHUC); American River near Natoma. Moist sandbar. Sept. 21, 1950, R. Tofsrud s.n. (AHUC); **Stanislaus Co.:** edge of Tuolumne River 3 miles SW of La Grange, wet soil. Aug. 23, 1961, P. Allen s.n. (JEPS); **Tuolumne Co.:** W side of Hetch Hetchy Dam, Swamp Lake Area, Yosemite NP. Aug. 9, 1958, H.L. Mason 14855 (UC); **Yolo Co.:** Common among rocks, east levee of Merritt Island, at Rd 142, SE corner of County. July 22, 1972, C. Quick 72-12 (AHUC): **NOTES:** Current determination of *P. Allen* s.n. by M. G. LeLong, 1995; previous determinations include *P. lindheimeri* Nash. and *P. agrostoides* Spreng. Included in Oswald and Ahart (1995, pg. 290) as a synonym of *P. acuminatum* var. *lindheimeri* (Nash) Fern.

**Panicum texanum Buckl.:** DIST: SnJV: CS: TEN: DOC: **Fresno Co.:** In a vineyard along Academy Ave. near Sanger. August, 1983, B. Fischer s.n. (AHUC), det. by B. Crampton, 1983; **Kern Co.:** Weed in vineyard, Delano. Sept., 1992, H. Kempen s.n. (DAV), det. by G.F. Hrusa, 1992: **NOTES:** An uncommon agricultural weed, sometimes treated in *Urochloa*, and so filed at DAV.

**Pennisetum glaucum (L.) R. Br.:** DIST: SnJV: CS: C: DOC: **Merced County:** Highway 33 about 3 miles S of southern outskirts of Gustine; moist roadside ditch near Main Canal at Pfitzer Road; T08S, R09E, Sec 29, MD. 37°12'28"N; 121°00'37"W; Howard Ranch quad., elev. 110 ft. With *Paspalum dilatatum*, *Sorghum halepense* dominant. July 12, 2000, D.W. Taylor 17480 (JEPS): **NOTES:** Escape from cultivation? Large areas were being grown (presumably for dairy silage) within about a half mile upstream of the site above. Although there was a sizable population, the occurrence could be attributed to seed washing downslope along the ditch alignment. In the Jepson Manual (pg. 1296), this name was misapplied to *Setaria pumila* (Poir.) R. & S. as the synonymized combination *Setaria glauca* (L.) P. Beauv.

**Pennisetum latifolium Spreng.:** DIST: CCo: CS: NCI:

**DOC: Santa Cruz Co.:** three clumps of plants to 12 ft, naturalized on shoulder of Southern Pacific RR just N of 30th Ave. crossing, Santa Cruz. Sept. 29, 1969, J. Bauer s.n. (CDA); loc. cit. Oct. 9, 1969, T.C. Fuller 18980 (CDA, DAV, UC); **Yolo Co.:** Davis, UC farm, volunteer in row A12 of grass garden. Oct. 25, 1923, P.B. Kennedy s.n. (AHUC).

**Phalaris coerulescens Desf.:** DIST: SnFrB: CS: C: DOC: **Contra Costa Co.:** Mount Diablo, Black Hawk Ridge Road south of Sycamore Creek, single plant on roadside. June 12, 1999, B. Ertter 16713 (JEPS): **NOTES:** Like *P. paradoxa*, but perennial with bulbous based culms, sterile spikelets not clublike. Not relocated in 2000, possibly due to road grading at the site.

**Phyllostachys aurea A. & C. Riviere:** DIST: SCo: CS: NCI: DOC: **Placer Co.:** Open dry slope above wash, 2 mi W of Auburn. Nov. 13, 1969, B. Crampton 8531 (AHUC); **Stanislaus Co.:** Colony established along permanent stream, La Grange Dam Rd 1 mi E of La Grange. June 20, 1969, P.S. Allen 429 (DAV); **Ventura Co.:** Poplar grove and thicket at juncture of San Antonio Creek and Ventura River near Arnaz Apple Orchards, Oak View. Re-collected after 15 yr in same spot. Colony enlarged. Dec. 21, 1962, H.M. Pollard s.n. (AHUC, CAS, CDA, SBBG).

**Phyllostachys bambusoides Siebold & Zuccarini:** DIST: CCo: CS: NCI: DOC: **San Mateo Co.:** McClintock, E., et al. (1990, pp. 181–182).

**Piptochaetium stipoides Hackel ex Arech. sensu lato:** DIST: NCo: CS: NW: DOC: **Marin Co.:** About ¼ mile E of Hwy 1 on trail to Bolinas Ridge, just north of road to Alpine Dam. May 9, 1978, C. Best s.n. (CAS, CDA); single plants or patch to 3 meters across, S-facing slope of canyon on W slope of Bolinas Ridge, 0.5 km E of Hwy 1 at southern limits of Dogtown. T01N, R08W, Sec. 11, MD. June 2, 1978, G.D. Barbe 2392 (CDA); loc. cit. G.D. Barbe 2391 (cited in correspondence, specimen location unknown), determinations by Gladys Perez-Camargo (BAA), B. Rosengurt (MVFA), and L.T. Ellis (K); infrequent patches to 10 meters across, S facing slope W of Bolinas Ridge, betw. Coppermine and Wilkins gulches at Dogtown (Woodville), 4 km N of Bolinas. Elev. 121 m. T01N, R08W, Sec. 11, MD. May 16, 1979, G.D. Barbe 2502 (CDA, DAV, UC); Ridge between Garden Canyon and Pike County Gulch on western slope of Bolinas Ridge ca. 3.25 miles north of Stinson Beach. Occasional in hard packed soil of old road. May 17, 1978, T.H. Harris s.n. (DAV): **NOTES:** Numerous more recent collections from the same localities above are at UTC. It is interesting that although the original California specimens of the *P. stipoides* alliance were determined as var. *purpurascens* (Hackel) Parodi, study of the associated correspondence indicated considerable variation among these specimens. Intraspecific application within the *P. stipoides* group is currently in dispute; and in addition, Barbe 2392 was originally det. at K as *P. grisebachii* (Speg.) Herter. Subsequent annotations at SI by E.G. Nicora indicate all were part of *P. stipoides* var. *purpurascens*. More recent collections determined by E. Sanchez (BA) again indicate two taxa are present at this site: *P. stipoides* var. *purpurascens* and var. *stipoides*. Apparently further field study on Bolinas Ridge would be useful. Well-established there where it is mixed with *P. setosum*. The land was private with restricted access until two years before the first collections in 1978, thus the species has possibly been present on the site for a considerable time. Speculated to have been introduced with cattle from S. America.

**Polypogon imberbis (Phil.) Bjorkm.:** DIST: CCo: CS:

NCI: **DOC: Contra Costa Co.:** near Martinez. June 7, 1900, *Burt Davy 6662* (US); **San Luis Obispo Co.:** Oceano Beach in moist spots among sand dunes. July 18, 1947, *R.F. Hoover 7314* (OBI, US); **NOTES:** Included in the Jepson Manual as *P. elongatus* Kunth, based on the two specimens cited above. Both of these recently re-determined by Robert Soreng (US) as *P. imberbis*. Hoover for San Luis Obispo Co. (1970) and especially Mason (1957) were uncomfortable with the *P. elongatus* determinations but did not suggest an alternative name.

**Pseudosasa japonica** (Sieb. & Zucc. ex Steud.) Makino ex Naka: **DIST:** CCo: **CS:** NCI: **DOC: San Francisco Co.:** Howell, J.T. et al. (1958, pg. 43); Thomas, H. (1961, p. 75); **NOTES:** Spreading vegetatively from cultivation.

**Schedonnardus paniculatus** (Nutt.) Trel.: **DIST:** CaR: **CS:** NCI: **DOC: Siskiyou Co.:** fence-line grass, Ager Road, Montague. Aug. 5, 1980, *D.H. Shaw s.n.* (AHUC, CDA).

**Spartina anglica** C.E. Hubb.: **DIST:** CCo: **CS:** NW: **DOC: Marin Co.:** Creekside Park adjacent to Corte Madera Creek, Greenbrae. Growing in low-flow channel of coastal salt marsh, assoc. with *Distichlis spicata* and *Spartina densiflora*. May 6, 2000, *S. Klohr s.n.* (CDA, DAV); **NOTES:** Only known site in California. More likely introduced to Creekside Park during marsh restoration work in 1977 sensu Spicher and Josselyn (1985) than via natural dispersal from Washington sensu Bossard et al. (2000).

**Stipa capensis** Thunb.: **DIST:** DSon (Coachella Valley): **CS:** NW: **DOC: Riverside Co.:** Coachella Valley/San Jacinto Mtns. Foothills. Alluvial fan of Chino Canyon along the Palm Springs tram road, N of the road 14 telephone poles above Hwy 111 (Palm Canyon Dr.), elev. 300 m/950 ft, 33°51'N; 116°34'W, T04S R04E Sec. 04, SB. Creosote bush scrub on rocky alluvium cut by arroyos; with *Larrea*, *Hymenoclea*, *Hyptis*, *Ambrosia*, *Justicia*, etc., three patches seen, ca. 200–300 individuals. Mar. 19, 1995, *A.C. Sanders 16148*, with *G. Helmkamp*, *P. MacKay*, et al. (UCR), det. by M. Barkworth; loc. cit. Apr. 6, 1995, *A. C. Sanders and M. Skinner 16393* (UCR); Coachella Valley, Chino Cyn., foothills of the San Jacinto Mtns., along the road to the Palm Springs Tram 1.5 mi above Hwy. 111. Palm Springs 7.5' quad., 33°50'34"N; 116°34'51"W, T04S, R04E, Sec. 04, SB. Elev. 1200 ft/366 m, rocky loam on alluvial fan, creosote bush scrub with *Larrea*, *Ambrosia dumosa*, *Opuntia echinocarpa*, *Krameria grayi*, etc., common annual on roadside and spreading into desert vegetation. Apr. 15, 2000, *A.C. Sanders 23321*, with *Giles Waines*, *Mitch Provance*, *T.B. Salvato*, et al. (UCR); Cathedral Canyon, border of Rancho Mirage [and] Cathedral City, 33°45'N; 116°30'W. Mar. 11, 1997, *Denise Woodard and Gilbert Goodlet s.n.* (UCR), det. by A.C. Sanders; San Jacinto Mtns., S of Chino Canyon, at NW end of Palm Springs, 33°50'20"N; 116°33'45"W, T04S, R04E, Secs. 09 and 10, SB. Elev. 1148 ft/350 m, flat areas with *Hyptis*, *Psoralea schottii*, some creosote bush and smoke trees, locally abundant in disturbed places. Mar. 18, 1997, *J. Wear and N. Moorhatch s.n.* (UCR), det. by A.C. Sanders; **NOTES:** First records for California and North America of this annual *Stipa* with long awns and sharp callus tips. This species will be a severe nuisance if it becomes widely established. The seeds readily become caught in the fur of dogs and other animals and so will probably create veterinary problems, and will certainly be subject to ready dispersal. The very sharp callus can easily pierce human skin and cause unpleasant sores. This plant is obviously a *Stipa* in the broad

sense, but its distinctly annual habit will quickly distinguish it from all other known Californian Stipeae. Acc. to M. Barkworth, in the narrow taxonomic sense this plant is an *Achnatherum*, but the published combination in that genus by P. Beauv (Essai Agrostogr. 146) is invalid, having as its basionym *Milium capense* L. and not *Stipa capensis* Thunb. Thus, in *Achnatherum* there is not currently an available epithet.

**Themeda quadrivalvis** (L.) Kuntze: **DIST:** SCo: **CS:** TEN: **DOC: San Bernardino Co.:** City of Ontario; private residence, southeastern corner of yard beneath power lines. Nov. 24, 1991, *T.S. Ross 6026* (CDA, RSA).

**Tribolium obliterum** (Hemzl.) Renvoize: **DIST:** CCo: **CS:** NW: **DOC: Monterey Co.:** well-established on sand dunes in scattered locations about the former Fort Ord Army base. June 6, 2000, *B. Delgado, E. Finley, B. Oliver s.n.* (CDA, DAV); Matthews, M.A. (1997, p. 341); loc. cit. April 17, 1990, *V. Yadon H-3828* (PGM); loc. cit. April 14, 1998, *V. Yadon H-3695* (PGM); **NOTES:** First collected by V. Yadon (PGM). *Sieglingia decumbens* (L.) Bernh. [= *Danthonia decumbens* (L.) DC.] misapplied. Reported in Matthews (1997) under that name. First records for North America. Native to South Africa.

**Triticum aestivum** L.: **DIST:** CA-FP: **CS:** C: **DOC: Alameda Co.:** Anthony Chabot Regional Park, archery range. June 2, 1981, *J. Stratford s.n.* (JEPS); **Fresno Co.:** Big Creek, 5000 ft. Aug. 9, 1956, *H.M. Pollard s.n.* (DAV, SBBG); **Humboldt Co.:** Arcata waste area near Community center. Apr. 14, 2000, *G. Leppig 1293* (CDA, HSC); **Kern Co.:** Twisselmann (1956, pg. 211); **Los Angeles Co.:** San Gabriel Mtns, Glendora Mtn. Rd., int. with Upper Monroe Rd. Rd. margin and adjacent vegetation. Locally naturalized. May 8, 1992, *T. Ross 6305* (UC); **Marin Co.:** Penalosa, J., (1963, pg. 27); Howell, J.T. (1970, p. 74); **Mendocino Co.:** nr. Walkers Valley. May 25, 1899, *J. Burt Davy and W.C. Blasdale 5062* (UC); **Monterey Co.:** roadside on Dolon Rd at Elkhorn Rd, May 24, 2000, *G. Leppig 1383* (CDA, HSC); **San Francisco Co.:** Howell, J.T. et al. (1958, pg. 45); **San Luis Obispo Co.:** Appearing from straw used to stabilize planted areas on sand dunes immed. W of Oso Flaco Lake. Elev. 150 ft. Apr. 5, 1987, *A.P. Griffiths 18086* (CDA, OBI); loc. cit. May 18, 1987, *A.P. Griffiths 18187* (CDA, OBI); **San Mateo Co.:** McClintock, E., et al. (1990, pg. 184); **Santa Barbara Co.:** Santa Barbara, N of Botanic Garden, Mission Cyn. Cr. June 19, 1944, *C.F. Smith 945* (DAV, SBBG); **Sonoma Co.:** Best, C., et al. (1996, pg. 312); **NOTES:** The above list is not exhaustive. As a casual, this species is relatively commonly encountered and can be expected throughout California; it is likely known from every county. Probably the most common introduction vector is straw bales used for roadside erosion control, but also may be a contaminant or a component of seeding mixes. It is popular for use as the latter because of its usually ephemeral nature. Although individual sites rarely persist, new locations appear regularly. Naturalization has been reported however, as in *Ross 6305* above (Los Angeles Co.), and its extent should be investigated further.

#### Pontederiaceae

**Heteranthera rotundifolia** (Kunth) Griseb.: **DIST:** ScV: **CS:** N: **DOC: Butte Co.:** Oswald, V.H. and L. Ahart, (1994, pg. 297); **Yuba Co.:** Damp soil in rice field, S of Woodruff Lane, just E of Mathews Rd, E of Sam Shintaffer's rice dryer, approx. 5 mi NE of Marysville. Common. Elev. 80'. T16N, R04E, MD. Sept. 17, 1999, *L. Ahart 8241* (CDA, CHSC).



## FIELD ASSESSMENT OF THE CALIFORNIA GAP ANALYSIS PROGRAM GIS DATABASE IN CENTRAL CALIFORNIA

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### ABSTRACT

Given the key role played by biogenic volatile organic compounds (BVOCs) in photochemical smog formation and atmospheric chemistry, it is critical to generate accurate BVOC emission inventories. Assembling such inventories requires reliable characterization of the areal coverage of plant species to quantify the leaf mass of BVOC-emitting vegetation. A recent GIS-based description of vegetation coverage in the natural areas of California is provided by the Gap Analysis Program (GAP) database. We conducted an assessment of this database in Central California through ground-based vegetation surveys to evaluate the use of GAP for developing a BVOC emission inventory for Central California. A modified stratified randomized sampling design was used to select and assess 18 GAP polygons. Quantitative vegetation surveys were conducted along belt transects in polygons dominated by trees and along line transects in polygons dominated by shrubs to determine percent cover of plant species for comparison to GAP data. The species listed by GAP accounted for a range of 0–88% of the relative cover in the polygons, with a mean of 43%. Of the 76 species listed by GAP for primary, secondary and tertiary assemblages for which data were collected (those species above the survey height), 33 were found to be correctly listed within their respective assemblages, 13 were found to be listed for the wrong assemblage, and 30 were below percentages of co-dominants of any assemblage. In the 18 polygons, a total of 51 additional species not listed by GAP were found to be present in amounts sufficient to consider them as potential co-dominants. Summed over all 18 polygons, BVOC emission indices based on field data were 20% less than those based on GAP, but for individual polygons differences ranged from –100% to more than +100%.

**Key Words:** Vegetation survey, biogenic hydrocarbons, Gap Analysis Program, GAP, BVOC.

BVOC emission inventories require data for emission rates, areal coverage, and leaf mass of respective plant species. With the proposal of a taxonomic methodology for assigning isoprene and monoterpene emission rates to unmeasured plant species (Benjamin et al. 1996), emission rates can in principle be estimated for many of the 6,000 plant species in California based on measurements within respective families and genera (Karlik and Winer 2001a; Winer and Karlik 2001). For California, vegetation spatial distribution and composition has been described for urban and natural areas within Orange County and the non-desert portions of Los Angeles, Riverside, and San Bernardino Counties (Winer et al. 1983; Miller and Winer

1984; Horie et al. 1991; Benjamin et al. 1997), and limited studies of plant composition have also been conducted for the Phoenix, AZ, urban area (Karlik and Winer 2001b) and the urban areas of Santa Barbara and Ventura Counties (Chinkin et al. 1996). However, a validated inventory of vegetation species composition and spatial distribution, specifically to develop a BVOC emissions inventory, has not been established for the extensive areas of natural vegetation in the San Joaquin Valley air basin.

A potential source of information concerning vegetation in the natural areas of the Central Valley and the Sierra Nevada is the Gap Analysis Program (GAP) database, which is coordinated by the United States Geological Service–Biological Resources Division (formerly the National Biological Service) to identify the distribution and management status of plant communities, especially to identify gaps in

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habitats for plant or animal species needing protection. GAP compiled a geographic information system (GIS) database (based primarily on remote-sensing data) describing vegetation type and dominance in terms of areal coverage (Davis et al. 1994, 1995). Unlike other vegetation maps which describe plant geography only in terms of plant communities, the California GAP database describes vegetation in quantitative terms using dominant plant species and species assemblages.

Because BVOC emissions inventories rely on species-specific measurements of both leaf mass and BVOC emission rates (Benjamin et al. 1997), GAP offers the advantage of providing species-specific vegetation distribution data. Moreover, the GAP GIS database is recent for California (Davis et al. 1995) and provides seamless coverage of the state. Although large-area small-scale GIS databases based on remote-sensing data, such as GAP, offer a potentially inexpensive and relatively simple approach to characterizing the distribution and species identities of natural vegetation within an airshed, use of such GIS databases for BVOC emissions inventory development requires evaluation of their accuracy and reliability for this purpose through ground-based observations.

The present GAP validation study was modeled after a previous study conducted in San Diego County (Winer et al. 1998; Chung and Winer 1999). Quantitative vegetation surveys were conducted along belt transects in polygons dominated by trees, and along line transects in polygons dominated by shrubs, in order to determine percent cover of major plant species for comparison with GAP listings.

We report here the results of a ground-based assessment of the GAP database within the Great Valley and Sierra Nevada ecological regions using vegetation surveys of representative GIS polygons. The surveys employed a modified stratified random sampling approach and a survey protocol based in part on the recommendations of the developers of the GAP database (Stoms et al. 1994), and refinements from the preceding study of GAP in San Diego County (Chung and Winer 1999). Data gathered from field surveys conducted during the 1999 and 2000 summers were used to assess the accuracy and concomitant utility of the GAP GIS database for providing quantitative information of plant species identities and coverages for BVOC emission inventories.

## METHODS

### Acquisition and Preparation of the GAP Database

As noted earlier, the purpose of GAP was to identify the distribution and management status of selected components of biodiversity. The central tool of this program was an ARC/INFO GIS database with plant species and vegetation class attributes associated with polygons within a defined

geographic region. This database was generated from summer 1990 Landsat Thematic Mapper satellite imagery, 1990 high altitude color infrared photography, vegetation type map surveys based on field surveys conducted between 1928 and 1940, and miscellaneous vegetation maps and ground surveys (Davis et al. 1995). Polygons were delimited based on climate, physiography, substrate, and disturbance regime. Landscape boundaries were subjectively determined through photointerpretation by expert personnel so that between-polygon variation was greater than within-polygon variation. The final result was a vegetation map with a 100 ha minimum mapping unit and a 1:100,000 mapping scale (Davis et al. 1995).

The GAP database for the southern portion of the Sierra Nevada and Great Valley ecological regions was obtained at the beginning of the project. Seven hundred forty-two polygons in the Great Valley and 1420 polygons in the Sierra Nevada ecological regions were found within the counties of Kern, Tulare, Kings, Fresno, and Madera. For each polygon in the database, a primary vegetation assemblage was listed. For most polygons a secondary vegetation assemblage was listed, and for some polygons a tertiary vegetation assemblage was also given. The primary assemblage was defined as the assemblage covering the majority of the polygon, and the secondary and tertiary assemblages as covering relatively smaller areas of the polygon. Each assemblage consisted of up to three co-dominant overstory species, each with a minimum of 20% of the relative cover of that assemblage. Relative cover of a given plant species within an assemblage was the fraction of total assemblage vegetation cover occupied by the given species.

### Polygon Selection

GAP data for each polygon were used to generate an isoprene and monoterpene index for the polygon (Winer et al. 1998; Chung and Winer 1999). Although polygons with high emissions indices may hold more interest for emissions modelers, after lengthy discussions and review of comments on a previous study design for GAP (Winer et al. 1998; Chung and Winer 1999), we decided to use a random selection process rather than focusing on "high emitting" polygons for field validation in this study. To remain a candidate for field validation, the polygon had to be below the atmospheric boundary layer, taken as 1800 m elevation, and within the San Joaquin Valley air basin. Further selection from the remaining polygons involved an iterative process accounting for feasibility, including physical access and permission to survey vegetation. A road map was overlaid on the area to see if there was access by roadways, and if so a universal transmercator (UTM) grid was generated. Polygons with a large public land component (e.g., within National Forest) were favored due to the rel-

TABLE 1. POLYGONS FROM THE GREAT VALLEY AND SIERRA NEVADA GAP DATABASE SELECTED FOR FIELD SURVEY.

Polygon		Approximate location	Area (ha)	Elevation (m)	Transect Type	Centerpt. (no.)	Transect (no.)
(no.)	GAP No.						
1	16541	Kern National Wildlife Refuge	1517	66	Line	4	16
2	17198	Kern River & Hwy 99	284	120	Belt	3	8
3	15485	Lemoore	256	64	Line	3	11
4	17023	Buttonwillow	254	82	Line	2	8
5	16442	Glennville	1383	1520	Belt	3	12
6	16753	Keyssville	195	1570	Belt	3	12
7	16908	Kern River Canyon	640	760	Belt	3	12
8	14572	Sequoia National Park	4431	1280	Belt	3	12
9	16791	Bodfish	309	1200	Belt	3	12
10	16273	California Hot Springs	2688	1570	Belt	4	14
11	13790	Sequoia National Park	635	1270	Belt	2	8
12	13795	Kings Canyon	2473	1340	Belt	1	2
13	16269	California Hot Springs	341	930	Belt	2	6
14	16687	Lake Isabella	1019	845	Belt	3	12
15	16783	Alta Sierra	476	1060	Belt	2	8
16	16776	Alta Sierra	642	1340	Belt	2	4
17	16756	Alta Sierra	1969	1080	Belt	2	4
18	16735	Alta Sierra	812	1030	Belt	2	4

ative ease of gaining permission to conduct surveys on such properties compared to privately owned properties.

Based on these criteria and the time and resources available for this research, 18 polygons in south central California were selected and surveyed for the present study, as seen in Table 1. Four polygons (nos. 1–4), located on the Central Valley floor, consisted primarily of shrubs and herbaceous vegetation, and fourteen polygons (nos. 5–18), located in the Sierra Nevada mountains and foothills, consisted primarily of woodland and forest vegetation (Fig. 1).

A subsample of polygons was selected as a test for correctness of the geographic location of a specific GAP polygon; in other words, a test of the registration of the GAP database. Three surrounding polygons adjacent to polygon 15 were selected for survey during the summer, 2000, sampling season. The plants found in these surrounding polygons could then be compared with those listed for the center polygon to see if plant communities listed for the center polygon were found instead in a surrounding polygon. The three surrounding polygons were no. 16 located to the southeast, no. 17 located on the western end, and no. 18 located to the northeast of polygon 15.

#### Selection of Sample Elements

If permission was obtained to access most of a polygon, sample elements of 500 × 500 m squares were selected by overlaying a 500 × 500 m UTM grid on the polygon, assigning sequential numbers to every grid square within 1 km of a road, and randomly selecting the centerpoint locations for the needed number of elements. The number of centerpoints and corresponding elements varied with

polygon size. For polygon areas of <1000, 1000–10,000, and >10,000 ha, two, three, and four centerpoints were chosen, respectively, although terrain or accessibility sometimes limited the number of centerpoints. This method was similar to the one employed in the Utah GAP validation project (Edwards et al. 1995) and that of Chung and Winer in San Diego County (1999). In several cases, suitable survey sites were not available within the vicinity of a road, so hikes of up to two hours along a trail were needed to reach the desired area within the polygon.

#### Vegetation Survey Protocol

The specific survey protocol chosen depended on the type of vegetation being assessed. Within the polygons dominated by trees, surveys were performed by a team of two along 6 m wide, 500 m long belt transects orthogonal at the centerpoint in most elements. Six meter wide belt transects make the mechanics of sampling easier while not significantly compromising accuracy (Lindsey 1955). For these belt transects, the surveyors walked 250 m north, south, east, and west away from the centerpoint, using a magnetic compass to maintain course.

Within polygons dominated by shrubs, the survey for each element consisted of two 300 m line transects orthogonal at the centerpoint. Line transects have been used to estimate relative cover for chaparral (Bauer 1943) and for sage scrub (Kent and Coker 1992; Zippin and Vanderwier 1994). The minimum square-shaped area needed to encompass a sample element within a polygon was therefore 25 ha for forests and woodlands, and nine ha for scrub and chaparral.

The survey team located the centerpoint of a par-

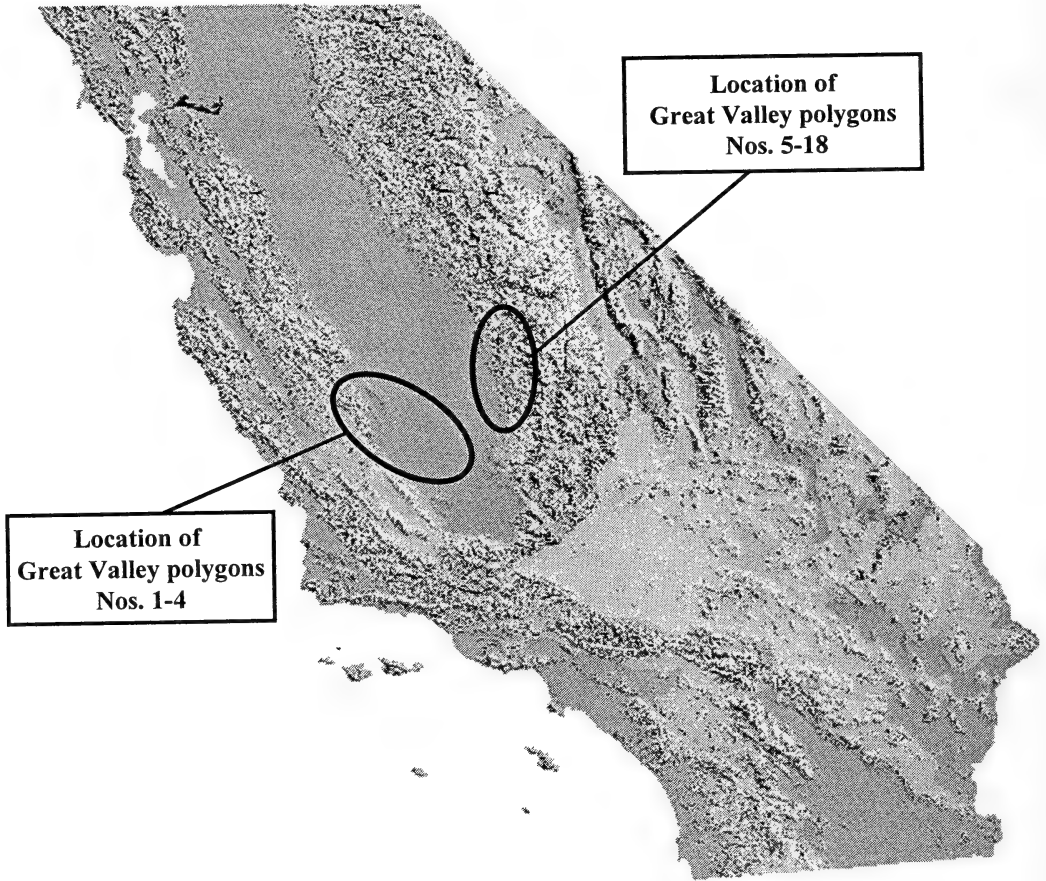


FIG. 1. Locations of the polygons selected for field survey from the GAP database.

ticular sample element using a global positioning receiver (GPS) locked onto UTM coordinates gathered from the GAP database. A handheld GPS unit (Garmin 12XL), with an accuracy of approximately  $\pm 15$  m or  $\pm 5$  m, in 1999 and 2000, respectively, was employed. Plant community and site descriptions were recorded and elevation at the centerpoint was determined using a hand-held altimeter (Pretel Instruments).

#### Data Collection

For belt transects, data collected included the crown radii, crown height, and diameter at breast height of trees and the crown dimensions of shrubs. For line transects, plant species identity, crown height and number of 0.1 m segments along a meter tape occupied by that plant species were noted. Plants such as grasses and forbs below a height of about 0.6 m were not recorded. Additional details of plant measurement methods have been reported previously (Winer et al. 1998; Chung and Winer 1999). Plant nomenclature follows Mabberley (1997).

#### Data Analysis

Data analysis followed the example of Chung and Winer (1999). For each polygon, the GAP database listed primary, secondary, and sometimes tertiary species assemblages and the estimated areal proportion ( $p$ ) of each assemblage within a polygon. Each species in a listed assemblage was a co-dominant, providing  $\geq 20\%$  relative cover within the assemblage. Therefore, the expected coverage of any species listed in the GAP database for a given polygon was  $\geq 0.2p$ . For example, in polygon 5 *Quercus kelloggii* was listed as a co-dominant in a primary assemblage that occupied 60–70% of the polygon. Using a mean value of 65% for  $p$ , GAP predicted *Quercus kelloggii* would cover  $\geq 0.2 \times 65\%$ , or  $\geq 13\%$  of the polygon.

The polygon coverage of plant species inferred from the GAP database by this procedure was compared with the cover data gathered from the field surveys in the 18 selected polygons. First, the coverage of each species within each sample element of a polygon was calculated. Then from the species coverage for each sample element, the mean cov-

erage and upper limit of the two standard error (SE) confidence intervals for the polygon were calculated, corresponding to an 85% confidence interval (McClave and Dietrich 1985).

## RESULTS

### Species Composition and Abundance within GAP Polygons

Table 2 summarizes results for the 18 polygons surveyed, listing the most abundant species observed for each polygon, the percent abundance predicted from the GAP database, the percent abundance determined by the field surveys, and the upper limits of a two SE interval of the percent composition. Plant species not listed by GAP or not found in surveys at  $\geq 1\%$  are omitted from this table, but may be found in the report of Winer and Karlik (2001). Total plant cover within the polygon ranged from as little as 7%, as found in polygons 2 and 9, up to 82% as found in polygon 12. In general, most of the sample cover in a polygon was attributable to a few species and many of the most abundant species found within the polygon were listed as co-dominants by the GAP database. However, the percentages of these GAP co-dominant species varied greatly. Total cover of GAP co-dominant species cover ranged from as little as 0% as found in polygon 18 up to 66% as found in polygon 12.

Relative cover of GAP-listed species compared to sampled species can be derived from the percentages listed in Table 2. For the Great Valley polygons (nos. 1–4), GAP species listings ranged from 29–72% of the plant species found. The sum of GAP species percentages for these polygons was 46, and for all species sampled, 100. Thus, GAP-listed plants accounted for 46% of the relative cover for polygons nos. 1–4 considered together. For the Sierra Nevada polygons (nos. 5–18), the relative cover of GAP-listed species for each polygon ranged from 0–88%, and the relative cover was 43% for polygons nos. 5–18 considered together. If all 18 polygons were considered together, GAP-listed plants accounted for 43% of the relative cover overall. To investigate whether GAP listings were more accurate for large vs smaller polygons, polygon size was multiplied by the corresponding percentages found for GAP-listed species vs for all species. The results suggested polygon size did not influence accuracy of GAP listings, since relative cover of GAP species was then found also to be 43%.

The observed sample cover of some co-dominants in GAP polygons often substantially exceeded the minimum predicted values. For example, in polygon 12 *Quercus chrysolepis* provided 51% of the polygon sample cover though  $\geq 7\%$  and  $\geq 3\%$  were predicted from the GAP listings for the secondary and tertiary assemblages, respectively. In polygon 5 *Quercus kelloggii* provided 31% of the

polygon sample cover when  $\geq 13\%$  was predicted by GAP.

In contrast, several polygons possessed co-dominant species that were found to be well under the predicted GAP percentages. For example, polygon 9 was found to have 1% mean sample cover of *Yucca whipplei* when GAP predicted the species to have  $\geq 11\%$  and  $\geq 7\%$  sample cover for the primary and secondary assemblages, respectively. In polygon 12, *Pinus ponderosa* was predicted by GAP to be found with sample cover  $\geq 11\%$  when the field study found it to be only 0.3% sample cover.

Because *Quercus* may be the most important genus of native woody plants with regard to BVOC emissions in California's airsheds, we compared the percentage of all oak species sampled to that inferred from GAP listings. For the 14 Sierra Nevada polygons (nos. 5–18), the mean coverage per polygon of oaks calculated from GAP listings was 17%, while from our field surveys oaks averaged 29% of the total cover. For all 18 polygons, the mean coverage of oaks calculated from GAP per polygon was 13% and from field surveys 22%. Since GAP listings give a lower limit for species abundances, one might expect to find oaks at the same or higher percentages than GAP listings. Considering polygons individually, for six of the 18 polygons we found oak species percentages within a factor of two of the respective GAP-predicted percentages. For an additional five polygons, oaks were listed as comprising zero percent cover, and were not found in the field surveys, in agreement with GAP listings. Thus, for 11 of 18 polygons, GAP listings for oaks were in reasonably good agreement with field data. For three polygons, nos. 8, 14, and 18, oaks were found at 20, 4, and 43% although no oak species were listed by GAP. Thus, overall GAP data were in reasonable agreement with field data, and the lower limit of oak coverages as given by GAP may underestimate oak abundance.

Since *Quercus* species vary over almost two orders of magnitude in isoprene emission rate (Csiky and Seufert 1999), the accuracy of oak species listings for any vegetation database is important for BVOC emission inventories. Using the data in Table 2, we considered oak species accuracy for each polygon by calculating the sum of absolute values of field percentage found for each oak species minus the respective percentage inferred from its GAP listing. These values for polygons ranged from 0% for the polygons where no oaks were listed or found to more than 40% for polygons 12, 15, 17, and 18 with a mean for all polygons of 19%. The accuracy of oak species listings did not appear to be related to polygon size.

We also evaluated the data in Table 2 with regard to non-oak genera and species considered to be moderate or high BVOC emitters, specifically those thought to have emission rates greater or equal to 10 or 2  $\mu\text{g g}^{-1} \text{h}^{-1}$  for isoprene and monoterpenes, respectively, as based on measured values or tax-

TABLE 2. MEASURED SPECIES COVER COMPOSITION OBSERVED IN SAMPLED GAP POLYGONS LISTED IN ORDER OF OBSERVED SAMPLED COVER. Species with mean sampled cover of <1% or not listed in GAP are omitted. N.D. = no data. For example, for *Avena* spp. and *Bromus* spp. species were observed but below survey height (about 0.6 m), and data were not recorded.

Polygon	Species	GAP predicted cover (%)	Mean sampled cover (%)	Sampled cover (s + 2SE) (%)
1	<i>Cyperus difformis</i>	—	17	30
	<i>Typha</i> spp.	≥11 & ≥3	15	38
	<i>Scirpus acutus</i>	—	6	17
	<i>Xanthium strumarium</i>	—	4	8
	<i>Brassica nigra</i>	—	3	7
	<i>Distichlis spicata</i>	—	3	6
	<i>Scirpus californicus</i>	—	1	3
	<i>Baccharis salicifolia</i>	—	1	2
	<i>Suaeda ramossissima</i>	—	1	2
	<i>Atriplex coronata</i>	—	1	2
	<i>Allenrolfea occidentalis</i>	≥7	1	2
	<i>Salix</i> spp.	≥7	0.2	0.6
	<i>Carex</i> spp.	≥11 & ≥3	0.0	—
	<i>Juncus</i> spp.	≥11	0.0	—
	<i>Tamarix</i> spp.	≥7 & ≥3	0.0	—
2	Total of sample cover		53	
	GAP co-dominants		16	
	Unknown #1	—	3	7
	<i>Populus fremontii</i>	≥7	2	3
	<i>Platanus racemosa</i>	—	1	2
	<i>Salix</i> spp.	—	1	2
	<i>Distichlis spicata</i>	≥13 & ≥7	N.D.	—
	Total of sample cover		7	
	GAP co-dominants		2	
	<i>Allenrolfea occidentalis</i>	≥17 & ≥3	21	43
	<i>Salix</i> sp.	—	9	27
	<i>Populus fremontii</i>	≥3	2	5
	<i>Eucalyptus</i> spp.	≥3	0.0	—
	Total of sample cover		32	
	GAP co-dominants		23	
3	<i>Atriplex polycarpa</i>	≥19	5	9
	<i>Adenostoma fasciculatum</i>	—	2	6
	<i>Avena</i> spp. and <i>Bromus</i> spp.	≥19	N.D.	—
	Total of sample cover		8	
	GAP co-dominants		5	
	<i>Quercus kelloggii</i>	≥13	31	41
	<i>Quercus wislizenii</i>	≥13 & ≥7	14	19
	<i>Quercus garryana</i>	≥7	6	17
	<i>Calocedrus decurrens</i>	—	5	9
	<i>Cercocarpus betuloides</i>	≥7	5	8
	<i>Abies concolor</i>	—	2	5
	<i>Pinus ponderosa</i>	≥13	1	2
	<i>Quercus berberidifolia</i>	—	1	1
	Total of sample cover		65	
	GAP co-dominants		57	
4	<i>Quercus kelloggii</i>	≥13 & ≥7	14	29
	<i>Pinus ponderosa</i>	≥13 & ≥7	6	13
	<i>Arctostaphylos</i> spp.	—	5	11
	<i>Quercus chrysolepis</i>	—	4	10
	<i>Abies magnifica</i>	—	3	6
	<i>Calocedrus decurrens</i>	—	2	7
	<i>Abies concolor</i>	≥13	1	3
	<i>Cercocarpus betuloides</i>	—	1	2
	<i>Quercus wislizenii</i>	≥7	1	1
	Total of sample cover		38	
	GAP co-dominants		22	

TABLE 2. CONTINUED.

Polygon	Species	GAP predicted cover (%)	Mean sampled cover (%)	Sampled cover (s + 2SE) (%)
7	<i>Quercus wislizenii</i>	—	7	13
	<i>Quercus douglasii</i>	≥7	3	3
	<i>Rhamnus crocea</i>	—	2	6
	<i>Ceanothus cuneatus</i>	—	2	5
	<i>Quercus garryana</i>	—	2	4
	<i>Platanus racemosa</i>	—	2	3
	<i>Pinus sabiniana</i>	≥7	2	3
	<i>Quercus dumosa</i>	—	1	4
	<i>Aesculus californica</i>	—	1	1
	<i>Adenostoma fasciculatum</i>	≥3	0.1	0.3
	<i>Avena</i> spp. and <i>Bromus</i> spp.	≥11	N.D.	—
	Total of sample cover		23	
	GAP co-dominants		5	
8	<i>Abies concolor</i>	—	13	31
	<i>Quercus douglasii</i>	—	9	28
	<i>Quercus kelloggii</i>	—	8	17
	<i>Calocedrus decurrens</i>	—	8	15
	<i>Ceanothus integerrimus</i>	—	4	13
	<i>Aesculus californica</i>	—	4	11
	<i>Quercus chrysolepis</i>	—	3	10
	<i>Pinus ponderosa</i>	≥17	3	8
	<i>Pinus lambertiana</i>	—	2	4
	<i>Cornus nuttallii</i>	—	1	4
	<i>Sequoiadendron gigantea</i>	—	1	3
	<i>Umbellularia californica</i>	—	1	2
	<i>Adenostoma fasciculatum</i>	≥3	0.0	—
9	Total of sample cover		58	
	GAP co-dominants		3	
	<i>Chrysothamnus nauseosus</i>	≥3	2	2
	<i>Juniperus californica</i>	≥7	1	2
	<i>Yucca whipplei</i>	≥11 & ≥7	1	1
	<i>Eriogonum fasciculatum</i>	≥11 & ≥7 & ≥3	0.2	0.3
	<i>Artemisia tridentata</i>	≥3	0.0	—
	Total of sample cover		7	
	GAP co-dominants		4	
10	<i>Quercus douglasii</i>	≥13 & ≥7	18	29
	<i>Aesculus californica</i>	≥7	13	17
	<i>Quercus wislizenii</i>	≥7	10	17
	<i>Quercus kelloggii</i>	≥13	9	26
	<i>Quercus garryana</i>	—	6	18
	<i>Quercus chrysolepis</i>	—	3	10
	<i>Cercocarpus betuloides</i>	—	3	6
	<i>Pinus sabiniana</i>	—	2	4
	<i>Rhus diversiloba</i>	—	1	3
	<i>Ceanothus cuneatus</i>	—	1	2
	<i>Ribes</i> sp.	—	1	2
	Total of sample cover		67	
	GAP co-dominants		50	
11	<i>Cercocarpus betuloides</i>	≥19	26	26
	<i>Ceanothus integerrimus</i>	—	20	56
	<i>Ceanothus cuneatus</i>	—	10	29
	<i>Quercus dumosa</i>	—	6	16
	<i>Aesculus californica</i>	—	3	9
	<i>Quercus chrysolepis</i>	≥19	2	6
	<i>Arctostaphylos</i> sp.	—	2	5
	<i>Umbellularia californica</i>	—	2	4
	<i>Arctostaphylos mewukka</i>	≥19	0.0	—
	Total of sample cover		71	
	GAP co-dominants		28	

TABLE 2. CONTINUED.

Polygon	Species	GAP predicted cover (%)	Mean sampled cover (%)	Sampled cover (s + 2SE) (%)
12	<i>Quercus chrysolepis</i>	≥7 & ≥3	51	—
	<i>Calocedrus decurrens</i>	≥11	51	—
	<i>Umbellularia californica</i>	—	9	—
	<i>Cercocarpus betuloides</i>	≥7	4	—
	<i>Ceanothus cuneatus</i>	—	2	—
	<i>Quercus dumosa</i>	—	2	—
	<i>Arctostaphylos</i> sp.	—	1	—
	<i>Salix</i> spp.	—	1	—
	<i>Pinus ponderosa</i>	≥11	0.3	—
	<i>Abies concolor</i>	≥11	0.0	—
	<i>Aesculus californica</i>	≥7	0.0	—
	<i>Pinus contorta</i>	≥3	0.0	—
	Total of sample cover		82	
13	GAP co-dominants		66	
	<i>Quercus wislizenii</i>	≥11 & ≥7 & ≥3	13	32
	<i>Aesculus californica</i>	≥11 & ≥3	10	20
	<i>Quercus douglasii</i>	≥11 & ≥7	8	23
	<i>Ceanothus cuneatus</i>	—	3	8
	<i>Quercus dumosa</i>	—	2	4
	<i>Umbellularia californica</i>	—	2	4
	<i>Fremontodendron californicum</i>	—	1	2
	<i>Cercocarpus betuloides</i>	—	1	1
	<i>Pinus sabiniana</i>	≥7	0.4	1
	<i>Avena</i> spp. and <i>Bromus</i> spp.	≥3	N.D.	—
	Total of sample cover		41	
	GAP co-dominants		31	
15	<i>Ceanothus cuneatus</i>	—	26	28
	<i>Pinus sabiniana</i>	—	18	45
	<i>Quercus douglasii</i>	—	8	13
	<i>Quercus wislizenii</i>	—	7	8
	<i>Quercus dumosa</i>	≥15	4	6
	<i>Ephedra californica</i>	—	3	5
	<i>Mimulus aurantiacus</i>	—	2	5
	<i>Yucca whipplei</i>	—	2	3
	<i>Adenostoma fasciculatum</i>	—	1	3
	<i>Juniperus californica</i>	—	1	1
	<i>Artemisia tridentata</i>	≥5	0.2	0.5
	<i>Avena</i> spp. and <i>Bromus</i> spp.			
	Total of sample cover		73	
16	GAP co-dominants		4	
	<i>Quercus kelloggii</i>	≥11	19	43
	<i>Quercus douglasii</i>	≥9	10	25
	<i>Quercus garryana</i>	—	8	23
	<i>Quercus dumosa</i>	—	8	23
	<i>Aesculus californica</i>	—	7	20
	<i>Quercus wislizenii</i>	—	3	10
	<i>Ceanothus cuneatus</i>	—	3	6
	<i>Pinus sabiniana</i>	—	2	5
	<i>Cercocarpus betuloides</i>	—	1	2
	<i>Pinus ponderosa</i>	≥11	1	3
	<i>Avena</i> spp. and <i>Bromus</i> spp.	≥11	N.D.	—
	Total of sample cover		63	
17	GAP co-dominants		30	
	<i>Ceanothus cuneatus</i>	—	11	11
	<i>Quercus lobata</i>	—	8	23
	<i>Quercus douglasii</i>	≥17 & ≥3	8	11
	<i>Aesculus californica</i>	—	7	20
	<i>Quercus wislizenii</i>	—	7	12
	<i>Quercus kelloggii</i>	—	6	19
	<i>Quercus garryana</i>	—	6	18



TABLE 2. CONTINUED.

Polygon	Species	GAP predicted cover (%)	Mean sampled cover (%)	Sampled cover (s + 2SE) (%)
18	<i>Quercus dumosa</i>	—	4	6
	<i>Ribes</i> sp.	—	2	6
	<i>Pinus sabiniana</i>	—	2	6
	<i>Cercocarpus betuloides</i>	—	1	1
	<i>Avena</i> spp. and <i>Bromus</i> spp.	≥3	N.D.	—
	Total of sample cover		62	
	GAP co-dominants		8	
	<i>Quercus douglasii</i>	—	25	40
	<i>Quercus wislizenii</i>	—	15	40
	<i>Aesculus californica</i>	—	9	21
	<i>Ceanothus cuneatus</i>	—	9	9
	<i>Quercus dumosa</i>	—	3	9
	<i>Pinus sabiniana</i>	—	1	2
	<i>Cercocarpus betuloides</i>	—	1	2
	<i>Adenostoma fasciculatum</i>	≥13	0.0	—
	Unidentified chaparral shrubs	≥5	N.D.	—
	Bare exposed rocks	≥3	N.D.	—
	Total of sample cover		63	
	GAP co-dominants		0	

onomy (Benjamin et al. 1996; Karlik and Winer 2001a). For the 11 polygons where such genera or species were listed, the field surveys gave percentages lower than those inferred from GAP for seven polygons, and higher than GAP for four polygons. For the seven polygons where no genera or species with moderate or high emission rates were listed, the field surveys found an absence of such genera or species in two polygons, and for the other five polygons percentages of emitting species ranged from 1–11% of total area. In considering the mean of GAP listings for BVOC-emitting species vs the mean of the field survey data for all 18 polygons, GAP predicted a mean coverage per polygon of 9% for these species, and field data were in good agreement with a mean of 8% of such species found. Thus, on average GAP data were harmonious overall with field observations for non-oak genera and species considered to be important BVOC emitters.

Correctness of GAP Listed Species within Species Assemblages

Species found within the polygons in the field were compared to their GAP listings and assessed for correct placement based on assemblage data, and the results are given in Table 3. A species was considered to be correctly listed when the percentage found in the field within two standard errors (s + 2SE, Table 2) exceeded the GAP-predicted percentage. A species was considered listed incorrectly when listed by GAP as a co-dominant in a particular assemblage (primary, secondary, and tertiary) but found at a lower percentage cover so as to place it within a different assemblage. Potential co-dominant species were defined as species not listed by

GAP as present in the polygon but found in field surveys to have cover percentage large enough to at least fall within the tertiary assemblage of a particular polygon. When GAP listed no species for the secondary or tertiary assemblage, an arbitrary value of ≥7% and ≥3% up to the next greater listed assemblage percentage were assigned, respectively, to identify potential species belonging to a particular assemblage. We note that GAP assigns minimum percentages to plant species coverages, but does not assign maxima; therefore, species listed in two or more coverage classes were considered to have a correct listing in these classes if present in sufficient quantity for the greater percentage requirement. For example, in polygon 6 the species *Quercus kelloggii* was listed in both primary and secondary assemblages, found to be present at 14%, and considered to be correctly listed for both assemblages.

The agreement of field results with GAP data varied among polygons, as seen in Table 3. There were several polygons (nos. 3, 5, 6, 10, 13) in which the field results agreed with all or the majority of GAP listings. In contrast, there were several instances where species listed by GAP in either the primary, secondary, or tertiary assemblage were not observed in the polygon in sufficient abundance for their respective assemblage. For example, in polygon 6 *Abies concolor* in the primary assemblage and in polygon 7 *Quercus douglasii* in the secondary assemblage were found with coverage percentages below those for their respective assemblages. Potential co-dominant species were noted in several polygons, such as in polygons 8 and 17, where seven species were found in percentages that

TABLE 3. SPECIES LISTED CORRECTLY AND INCORRECTLY WITHIN GAP POLYGONS SURVEYED. <sup>1</sup> GAP species listed incorrectly in plant assemblages = Species listed by GAP as a co-dominant in a particular assemblage (primary, secondary, and tertiary) but found within a different assemblage. <sup>2</sup> When GAP listed no species for the secondary assemblage an arbitrary value of  $\geq 7\%$  up to the primary percentage was assigned to identify potential secondary species. When GAP listed no species for the tertiary assemblage an arbitrary value of  $\geq 3\%$  up to the secondary percentage was assigned to identify potential tertiary species. <sup>3</sup> Species noted but below minimum height (0.6 m), and therefore not measured. <sup>4</sup> Species not observed.

	Primary, Poly- gon tertiary	GAP listing	GAP species listed correctly in plant assemblages	GAP species listed incorrectly in plant assemblages	GAP species observed below co-dominant percentages	Potential co-dominants not listed by GAP (percentage found) <sup>2</sup>
1	P	Carex spp. Juncus spp. Typha spp.			Carex spp. <sup>4</sup> Juncus spp. <sup>4</sup>	Cyperus difformis (17)
	S	Allenrolfea occidentalis Salix spp.	Typha spp.		Allenrolfea occidentalis Salix spp.	
	T	Tamarix spp. Carex spp. Tamarix spp. Typha spp.			Tamarix spp. <sup>4</sup> Carex spp. <sup>4</sup> Tamarix spp. <sup>4</sup>	Scirpus acutus (6) Xanthium strumarium (4) Brassica nigra (3) Distichlis spicata (3)
2	P	Distichlis spicata <sup>3</sup>				None
	S	Distichlis spicata <sup>3</sup> Populus fremontii		Populus fremontii		None
	T	None				Unknown #1 (3)
3	P	Allenrolfea occidentalis	Allenrolfea occidentalis			Salix sp. (9)
	S	Allenrolfea occidentalis Eucalyptus spp. Populus fremontii	Allenrolfea occidentalis Populus fremontii		Eucalyptus spp. <sup>4</sup>	
	T	None				None
4	P	Atriplex polycarpa Avena spp. & Bromus spp. <sup>3</sup>		Atriplex polycarpa		None
	S	None				None
	T	None				None
5	P	Pinus ponderosa Quercus kelloggii Quercus wislizenii	Quercus kelloggii Quercus wislizenii		Pinus ponderosa	None
	S	Cercocarpus betuloides Quercus garryana Quercus wislizenii	Cercocarpus betuloides Quercus garryana Quercus wislizenii			None
	T	None				Calocedrus decurrens (5)
6	P	Abies concolor Pinus ponderosa Quercus kelloggii	Pinus ponderosa Quercus kelloggii	Abies concolor		None

TABLE 3. CONTINUED.

Poly- gon	Primary, secondary, tertiary	GAP listing		GAP species listed correctly in plant assemblages	GAP species listed incorrectly in plant assemblages	GAP species observed below co-dominant percentages	Potential co-dominants not listed by GAP (percentage found) <sup>2</sup>
7	S	<i>Pinus ponderosa</i> <i>Quercus kelloggii</i> <i>Quercus wislizenii</i> None	<i>Pinus ponderosa</i> <i>Quercus kelloggii</i>			<i>Quercus wislizenii</i>	None  <i>Arctostaphylos</i> spp. (5) <i>Quercus chrysolepis</i> (4) <i>Abies magnifica</i> (3) None <i>Quercus wislizenii</i> (7)
	P	<i>Avena</i> spp. & <i>Bromus</i> spp. <sup>3</sup>					
	S	<i>Quercus douglasii</i> <i>Pinus sabiniana</i>		<i>Quercus douglasii</i> <i>Pinus sabiniana</i>			
	T	<i>Adenostoma fasciculatum</i>				<i>Adenostoma fasciculatum</i>	None
	P	<i>Pinus ponderosa</i>		<i>Pinus ponderosa</i>			
8	S	<i>Adenostoma fasciculatum</i>				<i>Adenostoma fasciculatum</i> <sup>4</sup>	<i>Abies concolor</i> (13) <i>Quercus douglasii</i> (9) <i>Quercus kelloggii</i> (8) <i>Calocedrus decurrens</i> (8) <i>Ceanothus integerrimus</i> (4) <i>Aesculus californica</i> (4) <i>Quercus chrysolepis</i> (3) None
	T	None				<i>Eriogonum fasciculatum</i> <i>Yucca whipplei</i>	None
	P	<i>Eriogonum fasciculatum</i> <i>Yucca whipplei</i>				<i>Juniperus californica</i> <i>Eriogonum fasciculatum</i> <i>Yucca whipplei</i>	None
	S	<i>Juniperus californica</i> <i>Eriogonum fasciculatum</i> <i>Yucca whipplei</i>				<i>Artemisia tridentata</i> <sup>4</sup> <i>Chrysothamnus nauseosus</i> <i>Eriogonum fasciculatum</i>	None
	T	<i>Artemisia tridentata</i> <i>Chrysothamnus nauseosus</i> <i>Eriogonum fasciculatum</i>					
9	P	<i>Quercus douglasii</i> <i>Quercus kelloggii</i>	<i>Quercus douglasii</i> <i>Quercus kelloggii</i>				None
	S	<i>Aesculus californica</i> <i>Quercus douglasii</i> <i>Quercus wislizenii</i> None	<i>Aesculus californica</i> <i>Quercus douglasii</i> <i>Quercus wislizenii</i>				None
	T	None					
	P	<i>Arctostaphylos mewukka</i> <i>Cercocarpus betuloides</i> <i>Quercus chrysolepis</i>	<i>Quercus chrysolepis</i>			<i>Arctostaphylos mewukka</i> <sup>4</sup>	<i>Quercus garryana</i> (6) <i>Quercus chrysolepis</i> (3) <i>Cercocarpus betuloides</i> (3) <i>Ceanothus integerrimus</i> (20)
	S						
10	P	<i>Quercus douglasii</i> <i>Quercus kelloggii</i>	<i>Quercus douglasii</i> <i>Quercus kelloggii</i>				None
	S	<i>Aesculus californica</i> <i>Quercus douglasii</i> <i>Quercus wislizenii</i> None	<i>Aesculus californica</i> <i>Quercus douglasii</i> <i>Quercus wislizenii</i>				None
	T	None					
	P	<i>Arctostaphylos mewukka</i> <i>Cercocarpus betuloides</i> <i>Quercus chrysolepis</i>	<i>Quercus chrysolepis</i>				
	S						
11	P	<i>Arctostaphylos mewukka</i> <i>Cercocarpus betuloides</i> <i>Quercus chrysolepis</i>	<i>Cercocarpus betuloides</i>		<i>Quercus chrysolepis</i>		
	T	None					
	S						
	P	<i>Arctostaphylos mewukka</i> <i>Cercocarpus betuloides</i> <i>Quercus chrysolepis</i>	<i>Cercocarpus betuloides</i>				
	S						

TABLE 3. CONTINUED.

Poly- gon	Primary, secondary, tertiary	GAP listing	GAP species listed correctly in plant assemblages	GAP species listed incorrectly in plant assemblages	GAP species observed below co-dominant percentages	Potential co-dominants not listed by GAP (percentage found) <sup>2</sup>
12	S	None				<i>Ceanothus cuneatus</i> (10)
	T	None				<i>Quercus dumosa</i> (6)
						<i>Aesculus californica</i> (3)
	P	<i>Abies concolor</i>			<i>Abies concolor</i> <sup>4</sup>	None
		<i>Calocedrus decurrens</i>	<i>Calocedrus decurrens</i>			
13	S	<i>Pinus ponderosa</i>			<i>Pinus ponderosa</i>	<i>Umbellularia californica</i> (9)
		<i>Aesculus californica</i>			<i>Aesculus californica</i> <sup>4</sup>	
		<i>Cercocarpus betuloides</i>		<i>Cercocarpus betuloides</i>		
	T	<i>Quercus chrysolepis</i>	<i>Quercus chrysolepis</i>			None
		<i>Pinus contorta</i>	<i>Quercus chrysolepis</i>		<i>Pinus contorta</i> <sup>4</sup>	None
14	P	<i>Aesculus californica</i>	<i>Aesculus californica</i>			None
		<i>Quercus wislizenii</i>	<i>Quercus wislizenii</i>			
		<i>Quercus douglasii</i>	<i>Quercus douglasii</i>			None
	S	<i>Quercus douglasii</i>	<i>Quercus douglasii</i>			
		<i>Quercus wislizenii</i>	<i>Quercus wislizenii</i>			
15	T	<i>Pinus sabiniana</i>			<i>Pinus sabiniana</i>	<i>Ceanothus cuneatus</i> (3)
		<i>Avena</i> spp. & <i>Bromus</i> spp. <sup>3</sup>				
		<i>Aesculus californica</i>	<i>Aesculus californica</i>			
	P	<i>Quercus wislizenii</i>	<i>Quercus wislizenii</i>		<i>Artemisia tridentata</i> <sup>4</sup>	None
		<i>Artemisia tridentata</i>		<i>Pinus sabiniana</i>		
16	S	<i>Pinus sabiniana</i>		<i>Pinus sabiniana</i>	<i>Artemisia tridentata</i> <sup>4</sup>	None
	T	None				
	P	<i>Quercus douglasii</i>		<i>Quercus douglasii</i>		<i>Ceanothus cuneatus</i> (6)
		<i>Adenostoma fasciculatum</i>				<i>Aesculus californica</i> (26)
	S					<i>Quercus wislizenii</i> (18)
17	T	None				<i>Quercus berberidifolia</i> (8)
	P	<i>Avena</i> spp. & <i>Bromus</i> spp. <sup>3</sup>			<i>Adenostoma fasciculatum</i>	<i>Ceanothus cuneatus</i> (7)
		<i>Pinus ponderosa</i>				<i>Quercus chrysolepis</i> (3)
		<i>Quercus kelloggii</i>	<i>Quercus kelloggii</i>			None
	S	<i>Quercus douglasii</i>	<i>Quercus douglasii</i>	<i>Pinus ponderosa</i>		None

TABLE 3. CONTINUED.

Primary, Poly- gon secondary, tertiary	GAP listing	GAP species listed correctly in plant assemblages	GAP species listed incorrectly in plant assemblages	GAP species observed below co-dominant percentages	Potential co-dominants not listed by GAP (percentage found) <sup>2</sup>
T	None				<i>Quercus garryana</i> (8) <i>Quercus dumosa</i> (8) <i>Aesculus californica</i> (7) <i>Quercus wislizenii</i> (3) <i>Ceanothus cuneatus</i> (3)
17	P	<i>Quercus douglasii</i>			None
	S	<i>Avena</i> spp. & <i>Bromus</i> spp. <sup>3</sup> <i>Quercus douglasii</i>	<i>Quercus douglasii</i>	<i>Quercus douglasii</i>	<i>Ceanothus cuneatus</i> (11) <i>Quercus lobata</i> (8) <i>Aesculus californica</i> (7) <i>Quercus wislizenii</i> (7) <i>Quercus garryana</i> (6) <i>Quercus kelloggii</i> (6) <i>Quercus dumosa</i> (4)
18	T	None			None
	P	<i>Adenostoma fasciculatum</i>		<i>Adenostoma fasciculatum</i> <sup>4</sup>	<i>Quercus douglasii</i> (25) <i>Quercus wislizenii</i> (15)
	S	Unidentified chaparral shrubs			<i>Aesculus californica</i> (9) <i>Ceanothus cuneatus</i> (9)
T		Bare exposed rocks			<i>Quercus dumosa</i> (3)

warranted co-dominant species designation, although none of these seven species was listed by GAP in any assemblage within the polygon.

Overall, as seen in Table 3, of the 76 species listed by GAP for primary, secondary and tertiary assemblages for which data were collected (those species above the survey height), 33 were found to be correctly listed within their respective assemblages, 13 were found to be incorrectly listed, and 30 were found to be below percentages of all co-dominants. Of these 30, 15 were not observed in the field at all. In the 18 polygons, six species not listed by GAP in any assemblage (within respective polygons) were found in field surveys to be potential primary species, 22 were found to be secondary, and 23 tertiary, for a total of 51 additional species not listed by GAP but found to be present in cover sufficient to be considered as potential co-dominants. The Great Valley polygons (nos. 1–4) did not seem to differ from the Sierra Nevada polygons (nos. 5–18) in accuracy of listings. Unlike the results of Chung and Winer (1999), we found the accuracy of listings of primary, secondary, and tertiary species was about the same (~40%) with, respectively, 14 of 32, 15 of 33, and 4 of 11 plants listed correctly.

Considering specifically data for oak species in Table 3, for the 18 polygons and for the 25 oak species listed, 20 were found to be listed correctly in their respective assemblages, three were listed incorrectly, and two were found to be below percentages for any co-dominant. Three additional oak species not listed by GAP were found to be potential primary co-dominants, 10 as secondary co-dominants, and nine as tertiary co-dominants. Thus, GAP listings for oaks were in good agreement with field data, but an additional 22 examples were found of oak species present at percentages large enough for inclusion as GAP co-dominants. Of these latter, the presence of two oak species in polygon 18 in percentages high enough to consider them primary suggests a significant discrepancy in cover type for that polygon between the listed species and field data. These results also indicate oaks may be found with greater spatial extent than inferred from the GAP database.

We also examined listings in Table 3 of genera and species, other than oaks, considered to be medium or high emitters of isoprene or monoterpenes. For the 18 polygons, and for the 14 listings for plants such as *Salix* spp. and *Populus* spp., three were found to be correct, four were incorrect, and seven were found to be below percentages of co-dominants. Field survey data indicated one species was found which could be considered a primary co-dominant, six could be secondary, and four tertiary. Therefore, 11 species of the medium or high emitters, were found at low percentages compared to their respective GAP listings, but 11 species not listed were found to be potential co-dominants,

which seem to be canceling errors in the database from the perspective of BVOC emissions.

As discussed earlier, the polygons surrounding polygon 15 were surveyed to test the GAP database for a possible registration error. The vegetation cover in polygons 16, 17, and 18 found in the field survey did not appear to match the GAP listings for polygon 15 any more closely than did the vegetation cover within the boundaries of polygon 15. Hence, in this case we found no evidence of mis-registration.

#### Implications of GAP Assessment Results for BVOC Emission Inventories in California

The primary purpose for GAP is to identify the distribution and management status of plant communities, rather than to identify individual plant species. The quantitative nature of GAP represents an advance in landcover classification and the values for plant cover and species percentages give an indication of the composition of plant communities. However, the GAP database is fundamentally about plant assemblages rather than species, and these assemblages may vary in precise composition depending on geographic and environmental factors. In addition, a component of leaf mass, which the GAP database does not provide, must be overlaid on the species distribution data for BVOC emission calculation. Thus, the applicability of GAP for BVOC modeling requires ongoing discussion.

We calculated isoprene emission indices (as described earlier) based on GAP data and found they differed less than  $\pm 50\%$  from the corresponding indices calculated from our field data for half the polygons surveyed. Isoprene emission indices summed over all 18 polygons based on GAP data were in good agreement with the sum of corresponding emission indices generated with data from field surveys, with a difference of only  $-6\%$  using field survey data vs GAP data. Results were not as consistent for monoterpenes. Ten of 18 polygons had monoterpene emission indices based on field survey data differing by less than 100% from those generated with GAP data, and the sum of monoterpene emission indices based on field surveys was 78% less than the sum calculated from GAP data. When field data were used in place of GAP data the sum of total isoprene and monoterpene emission indices dropped by 20%, and the change for individual polygons ranged from  $-100\%$  to more than  $+100\%$ . These percentage changes for the sum of emission indices were greater than those found in polygons assessed in San Diego (Chung and Winer 1999).

Compared to previous databases estimating percent cover of vegetation in natural areas, the GAP database is species-specific and has a higher spatial resolution. Results of this study, and that of Chung and Winer (1999), indicate GAP may be useful for assigning species identities to plant cover in the

natural areas of California airsheds for BVOC inventory development. However, GAP should be used for this purpose with caution, as there can be discrepancies in species listings for individual polygons resulting in considerable differences in estimated BVOC emissions.

#### Limitations of the Present Study

GAP assessment in the southern Central Valley and surrounding mountains posed special problems in terms of sampling representative areas within privately owned parts of a polygon. In the Utah GAP validation project, 42% of the state was under the control of the US Bureau of Land Management, with private interests owning 21% (Edwards et al. 1995). In the study of Chung and Winer (1999), the San Diego County Association of Government 1990 ownership database indicated private interests owned 41% of San Diego County land. In the present GAP assessment project, suitable public lands within the vicinity of roads were limited, resulting in extended hikes from established roads to reach them. Even with such effort, our ability to conduct surveys in representative areas of a polygon's major vegetation types as listed in the GAP database was limited.

Given the effort needed to gather the field data, it was necessary to limit the number of polygons assessed and the area sampled. Moreover, the sample area required for estimating the true sample cover of individual species in a polygon is not precisely known. One reference (Bormann 1953) suggested that surveying 7% of a forested area using parallel belt transects provided a 65% chance the sample mean of the basal area of the trees would be within 10% of the true mean for more common species. The effort needed to obtain an accurate measure of relative cover may be similar. In the present study, each sample element for belt transects occupied 0.6 ha, so for a polygon of 500 ha, two sample elements encompassing 1.2 ha were surveyed, or about 0.24% of the polygon area. For line transects, two sample elements in a 500 ha polygon would occupy about 1200 m<sup>2</sup>, or about 0.024% of the polygon.

On the other hand, the effective size of the samples may be larger. The vegetation cover composition within the transects may approximate the cover composition of a square which immediately bounds the ends of the perpendicular transects. In that case the percentage of the polygon area sampled would be 10% and 3.6% of a 500 ha polygon for belt and line transects, respectively.

#### CONCLUSIONS

A ground-based assessment of the GAP database for the Great Valley and Sierra Nevada ecoregions of California was conducted in the southern San Joaquin Valley and adjacent mountains to evaluate use of GAP in developing a BVOC emission in-

ventory for Central California. The species listed by GAP accounted for a range of 0 to 88% of the relative cover in the polygons, with a mean of 43%. Of the 76 species listed by GAP for primary, secondary and tertiary assemblages for which data were collected (those species above the survey height), 33 were found to be correctly listed within their respective assemblages, 13 were found to be listed for the wrong assemblage, and 30 were below percentages of co-dominants of any assemblage. In the 18 polygons, a total of 51 additional species not listed by GAP were found to be present in amounts sufficient to consider them as potential co-dominants. However, the listings of oak species and others considered to be important due to their magnitudes of biogenic emissions were generally in good agreement with field data. Summed over all 18 polygons, BVOC emission indices based on field data were 20% less than those based on GAP, but for individual polygons the differences ranged from -100% to more than +100%. Registration error did not seem to be the cause of discrepancies between listed and field data. Thus, this database should be used with caution for developing BVOC inventories. Other databases more limited in geographic coverage may also be useful, and should be validated for accuracy against field data, particularly for representativeness of species of interest.

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SOME FACTORS INFLUENCING SEEDLING DENSITY OF CALIFORNIA  
BLACK OAK (*QUERCUS KELLOGGII*) IN THE CENTRAL  
SIERRA NEVADA, CALIFORNIA

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ABSTRACT

Seedling densities of California black oak (*Quercus kelloggii*) and overstory and understory vegetation attributes were quantified on four 21.1-ha study stands in Placer County, California. California black oak seedlings differed among stands ( $P < 0.001$ ), and seedling densities (number/ha) at one stand (mean = 58,733) were 4.0–5.3 times more abundant than the other stands (mean = 11,133–14,400). Seedling density increased with increasing average diameters (cm) of surrounding California black oaks ( $P < 0.008$ ). Larger diameter oaks are older and produce more acorns that can germinate into seedlings than smaller diameter oaks. For the stand with the greatest seedling density, seedling density increased with increasing basal area ( $\text{m}^2/\text{ha}$ ) of California black oak ( $P = 0.028$ ). Variation in site conditions and the effects of California black oak diameters and basal area should be acknowledged when evaluating seedling densities and seedling-based recruitment for California black oak and prior to initiating management to promote seedling recruitment.

Key Words: *Quercus kelloggii*, recruitment, seedlings, California.

California black oak (*Quercus kelloggii*) is widely distributed throughout California's montane environments, and its distribution extends into west-central Oregon and northern Baja California (Griffin and Critchfield 1972; McDonald 1990). Occurring in mostly pure stands or mixed with conifers, California black oak is shade intolerant and a vigorous sprouter (McDonald 1969, 1990). Harvesting for firewood and saw logs is the land use most affecting this species, but California black oak remains mostly underutilized commercially despite its wide distribution and large timber volume (Bolsinger 1988; McDonald and Huber 1995). California black oak appears to be declining in some places as dying trees are not replaced because conifers are shading out oak seedlings and saplings in mixed-conifer stands, but not other places where oak sapling to tree ratios were adequate to support regeneration (Muick and Bartolome 1987; McDonald and Tappeiner 1996).

California black oak regenerates through stump sprouting or acorn germination. Sprouting is thought to be the primary regeneration method as stump sprouts grow fast to capture growing space, while acorn germination and growth into seedlings is thought to be an infrequent regeneration method

(McDonald 1969, 1990). Because of its sprouting ability, California black oak is thought to primarily occur in even-aged stands as fire and other disturbances are the primary way stands are replaced (McDonald 1969, 1990; McDonald and Tappeiner 1996), and sprouting maintains oak densities in existing stands if enough sprouts grow into mature trees.

Seedling occurrence is sporadic and has been associated positively with oak canopy cover and reduced solar radiation in woodlands (Standiford et al. 1997). Relationships between vegetation attributes and seedlings, however, have not been elucidated in forest habitats where timber management and fire suppression are dominant land uses. Germinated acorns change oak densities in existing stands as new trees are established, and acorns moved by animals away from parent trees can change oak distributions (Fuchs et al. 1997).

Understanding seedling density and occurrence patterns would help land managers design and implement management actions intended to maintain or enhance California black oak where sexual reproduction is favored. We observed four forest stands in the central Sierra Nevada with uneven-aged California black oak trees (Garrison et al. 2002) with variable amounts of seedlings. Given the lack of information on seedling densities from forest habitats, we undertook an investigation to

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document what stand attributes influenced California black oak seedling density in these four stands. Our objectives were to: (1) quantify seedling densities in stands dominated by mature, but various aged California black oaks; and (2) assess how seedling density is affected by vegetation attributes in these stands. The seedling investigation is part of a more comprehensive study of the dynamics of California black oak and wildlife population and community responses to habitat attributes in these same stands.

#### STUDY AREA

We conducted this study on four 21.2-ha study stands in Placer County, California. Elevations ranged from 1220–1320 m, and the stands were located on plateaus and upper portions of steep river canyons which characterized the study area. Study stands were located in larger size, homogeneous forest stands with a tree layer dominated by large diameter (>50 cm diameter breast height [dbh]) California black oak and ponderosa pine (*Pinus ponderosa*). Other less dominant tree species included interior live oak (*Q. wislizeni*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and incense cedar (*Calocedrus decurrens*). Seedling and sapling California black oak and ponderosa pine dominated the subcanopy at one stand, while the other stands had little subcanopy. The shrub layer was generally sparse, and deerbrush (*Ceanothus integerrimus*) and manzanita (*Arctostaphylos* spp.) were the most common shrubs. The herbaceous layer was dominated by a sparse to dense cover of mountain misery (*Chamaebatia foliolosa*) and seedlings of California black oak. California black oak was relatively widespread throughout the study area and occurred in stands with trees of all ages with varying amounts of conifers. The study stands were representative of those with mature, large diameter California black oak in the central Sierra Nevada, although these stands are rare in this area (Garrison et al. 1998).

#### METHODS

Seedling densities and associated vegetative characteristics were sampled from 30 0.04-ha plots in each stand (known as Stands 1–4). Each stand had two adjacent 10.6-ha subplots, and 15 0.04-ha circular plots were randomly selected and measured in each subplot at intersection points of a 25-m by 25-m grid. To ensure that the entire subplot was sampled, one circular plot was randomly located on each of 11 transects in the grid and sampled in July–August 1994. Four additional circular plots were selected from the same transects and sampled in July–August 1995 for a total of 15 circular plots per subplot and 30 circular plots per stand. Seedling and understory vegetation data were measured at all circular plots in 1995. Data were taken on di-

ameter (cm) and heights (m) of trees, cover (%) of the overstory canopy and understory, and stem densities (number/ha) and basal areas ( $\text{m}^2/\text{ha}$ ) of all live stems  $\geq 12.7$  cm dbh and  $\geq 2$  m tall. Seedlings (oaks <2.5 cm basal diameter) were counted from five 1-m<sup>2</sup> circular plots located at the 0.04-ha circular plot center and 5 m away from the plot center along axes pointing North (0°), East (90°), South (180°), and West (270°). Data were also collected on saplings (oaks 2.5–15 cm basal diameter and <2 m tall), but saplings occurred on 8% (10 of 120) of the vegetation plots so they were too rare to be analyzed.

Because most data did not meet assumptions and distribution requirements for parametric statistics, the data were transformed (Zar 1996). Log transformations ( $\log_{10} + 1.0$ ) (Zar 1996) were used for averages for seedling counts, basal area, stem density, heights and stem diameters for all trees, California black oak, and conifers. Cover for understory and overstory canopy were given arcsine transformations [arcsine radian degrees (square root (proportion canopy cover + 1))] (Zar 1996).

Analysis of variance with Bonferroni pairwise comparisons were used to determine differences among stands for the vegetation attributes. Pearson correlation coefficients for the transformed data was used to determine preliminary relationships between vegetation attributes and seedling densities with data from all stands combined and separately for Stand 1. While combining data from all stands for the correlations is considered pseudoreplication (Hurlbert 1984), the correlations were for exploratory purposes to select a smaller subset of habitat variables for more detailed analyses and no statistical inferences were made using these results.

Vegetation attributes with statistically significant ( $P < 0.05$ ) correlations were used in a backward stepwise general linear model to determine stand differences in seedling densities and which vegetation attributes had the greatest effect on seedling density. A multiple linear regression analysis was conducted for Stand 1 because it had the greatest seedling densities and frequency of plots with seedlings so it provided an opportunity to assess how habitat attributes influence seedling densities at the stand level. Understory cover measurements were not included in the general linear model or regression because two of the five understory attributes were highly correlated ( $P < 0.02$ ) with seedling density; this correlation indicated data interdependence and redundancy that biased relationships between the tree layer and seedlings. Statistical analyses were conducted using SYSTAT (SPSS Incorporated 1999). Summary statistics and scatterplots for each stand were used to assist interpretation of the general linear model results. Throughout this paper, the term “oak” is synonymous with California black oak as almost 100% of the tree oaks and 100% of the oak seedlings and saplings measured were California black oak.

## RESULTS

### Stand Attributes

The four stands consisted of relatively large diameter California black oaks and smaller diameter conifers with closed canopies, large amounts of basal area and moderate stem densities (Table 1). Sixteen of the 21 (76%) vegetation attributes measured differed ( $P < 0.024$ ) among the four stands. Stand 1 had greater oak seedling densities (#/ha), greater conifer tree densities (#/ha), greater oak understory cover (%), lesser oak tree densities (#/ha), smaller diameters (cm) of conifer trees, and shorter conifer trees (m) than the other stands ( $P < 0.001$ ). Stem densities, understory and overstory cover, tree diameters, and tree heights were the attributes that mostly differed among the stands ( $P < 0.024$ ) (Table 1). Basal area ( $\text{m}^2/\text{ha}$ ) of all trees and oak were similar ( $P > 0.197$ ) among stands. At all stands, 63–90% of the sample plots had at least one oak seedling indicating that some seedlings occurred over much of the area within and among stands (Fig. 1). Stands were at similar elevations (1220–1320 m); slopes varied from 5–30%, and aspects included E, SE, S, and W (Table 1).

### Habitat Attributes Affecting Seedling Densities

Of the 20 vegetation attributes analyzed for their possible effects on seedling densities at the four stands, seven (35%) attributes were correlated ( $n = 95\text{--}120$ ;  $P < 0.038$ ) with seedling density. Five of these seven attributes were from the tree layer (conifer tree density [#ha], oak basal area [ $\text{m}^2/\text{ha}$ ], average diameter [cm] of oaks and conifers, and average height [m] of oaks) and were used in the general linear model. The other two attributes (% total understory cover and % oak understory cover) are not included in the general linear model because they are highly correlated ( $n = 120$ ,  $P < 0.02$ ) and redundant variables for seedling density. At Stand 1, four (20%) of the 20 vegetation attributes (% oak and conifer overstory cover, oak basal area [ $\text{m}^2/\text{ha}$ ], and % oak understory cover) were correlated ( $n = 30$ ,  $P < 0.049$ ) with seedling density.

Average diameter (cm) of California black oak and stand were only attributes retained in the general linear model (Table 2). Seedling densities differed ( $P < 0.008$ ) among stands and increased ( $P < 0.001$ ) as average oak tree diameter increased (Table 2, Fig. 2). This relationship was due somewhat to the greater number of seedlings and larger diameter trees at Stand 1 (Table 1, Figs. 1 and 2). With Stand 1, seedling density increased with increasing oak basal area ( $P < 0.028$ ).

## DISCUSSION

California black oak seedlings were prevalent at one of four stands in the central Sierra Nevada, and the stands differed statistically in many vegetation attributes including densities, diameters, and

heights of trees. Oak seedling densities differed among stands and increased with increasing average diameters of the surrounding oak trees. More seedlings under larger diameter trees are expected because larger diameter California black oaks are older (Garrison et al. 2002) and acorn production increases with increasing age and diameter of California black oak (McDonald 1969; Garrison et al. in press). Older trees also have longer periods of time to deposit acorns on the ground that germinate into seedlings so greater numbers of seedlings accumulate under larger trees.

All stands were dominated by California black oak and had equivalent total overstory canopies, but slopes, aspects, and oak overstory canopy cover varied somewhat among stands. Presence of California black oak seedlings is negatively associated with solar radiation and positively associated with canopy cover of California black oak (Standiford et al. 1997), and probabilities of seedling occurrence at the four study stands were between 80–90% using the graphs from Standiford et al. (1997). Stand 1 had the greatest number of seedlings and the least amount of oak overstory cover (36%) as well as the least amount of solar radiation due to a relatively flat slope. Furthermore, seedling densities increased with increasing oak basal area in Stand 1. Although seedling densities increased with increasing oak diameter in plots from all four stands, oak basal area was also correlated ( $r = 0.194$ ,  $n = 120$ ,  $P < 0.034$ ) indicating that both vegetation attributes have affect seedlings.

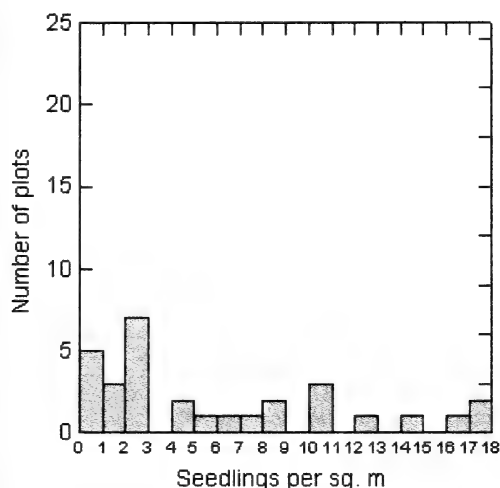
Seedling presence and abundance varies across small and large geographic areas as seedlings occurred on 63–90% of our survey plots in the central Sierra Nevada yet densities varied four to fivefold among stands. Other studies reported California black oak seedlings present on 83% of survey plots in the southern Sierra Nevada (Standiford et al. 1997) and 62% of sample plots in the range of the California black oak habitat in California (Bolsinger 1988).

Seedlings are germinated acorns, so acorn production by parent trees ultimately affects seedling densities. California black oak acorn production has considerable spatial and temporal variation (Koenig et al. 1994) so acorns are limited at certain sites and particular times. In our stands, plots with larger oaks had lower stem densities with varying amounts of canopy cover so germinating acorns and seedlings received varying amounts of sunlight. Acorns deposited in areas with lesser canopy cover germinate and grow at greater levels than acorns in areas with greater canopy cover (Savage 1994; Standiford et al. 1997), and this pattern occurred at Stand 1 where seedling densities were greatest at moderate (15–55%) canopy coverages. Seedling regeneration of California black oak is clumpy as seedlings concentrate around drip lines of parent trees (Savage 1994; McDonald and Tappeiner 1996). Furthermore, acorns are distributed and

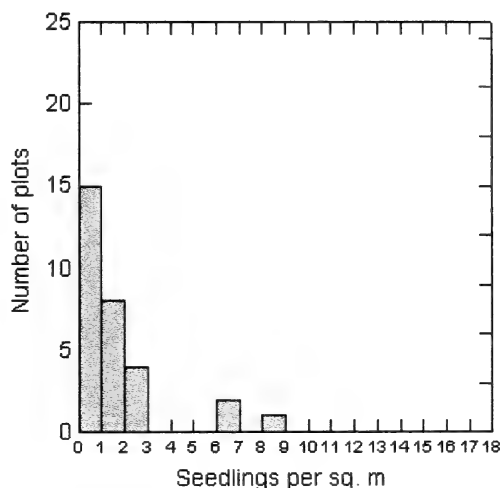
TABLE 1. CALIFORNIA BLACK OAK SEEDLING DENSITIES AND OTHER VEGETATION ATTRIBUTES (MEAN  $\pm$  SE) FROM 1994 AND 1995 AT FOUR 21.1-HA STANDS IN PLACER COUNTY, CALIFORNIA. Numbers with successive differing letters are different (ANOVA Bonferroni pairwise comparisons,  $P < 0.05$ ) from each other. <sup>1</sup> ANOVA—df = 3, 91–116. <sup>2</sup> ANOVA performed on seedlings/m<sup>2</sup> but presented as seedlings/ha for comparative purposes with other attributes.

	Stands				ANOVA <sup>1</sup>	
	1	2	3	4	F	P-value
	(n = 17–30)	(n = 15–30)	(n = 25–30)	(n = 25–30)		
Seedlings/ha <sup>2</sup>	58,733 $\pm$ 9,944 A	14,400 $\pm$ 3,815 B	11,133 $\pm$ 2,263 B	11,867 $\pm$ 4,374 B	16.03	0.001
Basal area (m <sup>2</sup> /ha)						
All trees	38.7 $\pm$ 3.8	30.9 $\pm$ 3.8	42.2 $\pm$ 4.4	40.1 $\pm$ 4.0	1.58	0.197
California black oak	19.7 $\pm$ 3.8	21.0 $\pm$ 2.8	21.4 $\pm$ 2.9	18.4 $\pm$ 2.4	0.38	0.784
Conifers	19.0 $\pm$ 3.6	9.9 $\pm$ 3.2 A	20.8 $\pm$ 4.4	21.7 $\pm$ 3.5 B	3.53	0.017
Stern density (number/ha)						
All trees	330.8 $\pm$ 29.0 A	193.3 $\pm$ 26.0 B	197.5 $\pm$ 22.4 B	301.7 $\pm$ 25.8 A	8.57	0.001
California black oak	57.5 $\pm$ 11.1 A	139.2 $\pm$ 19.6 B	104.2 $\pm$ 15.0 B	154.2 $\pm$ 21.6 B	7.66	0.001
Conifers	273.3 $\pm$ 31.5 A	53.3 $\pm$ 17.1 BC	93.3 $\pm$ 18.8 B	147.5 $\pm$ 23.5 BD	21.71	0.001
Overstory canopy cover (%)						
All trees	70.0 $\pm$ 3.3	70.7 $\pm$ 4.1	67.9 $\pm$ 4.2	75.3 $\pm$ 3.4	0.97	0.408
California black oak	36.2 $\pm$ 4.4 A	57.8 $\pm$ 5.0 B	47.1 $\pm$ 5.2	47.8 $\pm$ 4.5	3.27	0.024
Conifers	33.8 $\pm$ 4.4 A	12.9 $\pm$ 3.5 BC	20.8 $\pm$ 3.6	27.5 $\pm$ 3.6 D	7.27	0.001
Understory cover (%)						
Total	36.5 $\pm$ 3.5	27.1 $\pm$ 3.9	37.4 $\pm$ 3.7	33.1 $\pm$ 3.8	2.37	0.074
Mountain misery	17.1 $\pm$ 3.4	15.6 $\pm$ 3.1 A	17.4 $\pm$ 3.6	27.2 $\pm$ 3.4 B	3.47	0.019
California black oak	14.3 $\pm$ 2.0 A	1.4 $\pm$ 0.7 B	1.7 $\pm$ 0.7 B	1.3 $\pm$ 0.5 B	38.85	0.001
Forbs	4.0 $\pm$ 1.1 A	8.8 $\pm$ 2.2 C	15.8 $\pm$ 2.8 B	2.2 $\pm$ 0.8 D	13.71	0.001
Ferns	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.3 $\pm$ 0.2	0.0 $\pm$ 0.0	0.68	0.567
Stem diameter (cm)						
All trees	33.9 $\pm$ 2.0 A	45.3 $\pm$ 4.1	48.5 $\pm$ 3.2 B	37.6 $\pm$ 2.7	4.79	0.003
California black oak	63.6 $\pm$ 6.4 A	47.3 $\pm$ 4.4	49.2 $\pm$ 3.3	37.7 $\pm$ 2.5 B	4.11	0.008
Conifers	26.4 $\pm$ 1.6 A	46.1 $\pm$ 6.8 B	51.6 $\pm$ 5.6 B	43.1 $\pm$ 4.6 B	7.20	0.001
Tree height (m)						
All trees	15.9 $\pm$ 1.1 A	20.0 $\pm$ 1.2	22.7 $\pm$ 1.7 B	19.1 $\pm$ 1.7	4.43	0.005
California black oak	18.1 $\pm$ 1.2	19.2 $\pm$ 1.3	20.2 $\pm$ 1.4 A	14.8 $\pm$ 1.3 B	3.60	0.016
Conifers	14.9 $\pm$ 1.1 A	24.0 $\pm$ 2.3 B	26.8 $\pm$ 3.5 B	25.1 $\pm$ 2.7 B	4.73	0.004
Elevation (m)	1280	1225	1220	1320		
Aspect	W	E	S	E		
Slope (%)	5	20	30	30		

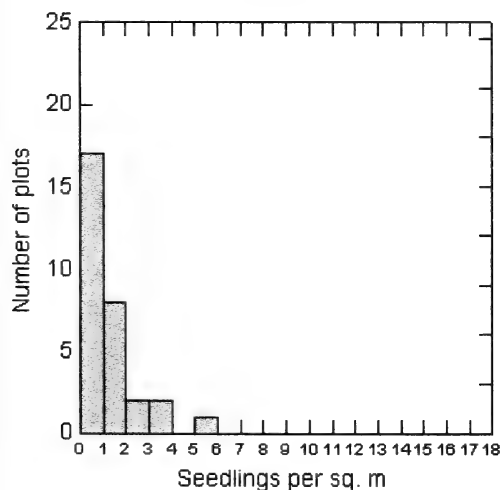
## Stand 1



## Stand 2



## Stand 3



## Stand 4

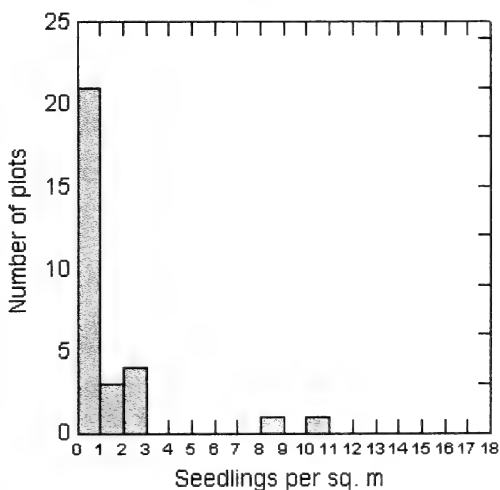


FIG. 1. Frequencies of plots with varying densities of California black oak (*Quercus kelloggii*) seedlings (number/m<sup>2</sup>) measured in 1995 at four 21.1-ha study stands in Placer County, California. The number of plots without seedlings in the 0–1 seedlings/m<sup>2</sup> density class were Stand 1 = 3, Stand 2 = 8, Stand 3 = 4, and Stand 4 = 11.

cached by western gray squirrels (*Sciurus griseus*) (McDonald 1969) and Steller's jay (*Cyanocitta stelleri*) (personal observation, Fuchs et al. 1997). Many cached acorns are not consumed by wildlife and then germinate into seedlings.

In undisturbed settings, regeneration of California black oak from germinated acorns occurs as a steady accumulation of seedlings rather than large pulses (McDonald and Tappeiner 1996), although seedlings must be aged to confirm this. Because

they grow slowly under the canopy of overstory trees, oak seedlings generally have similar heights although ages can be different (McDonald and Tappeiner 1996). Seedling accumulations were obvious at Stand 1, but seedling ages were not determined to confirm whether they had accumulated over many years or resulted from a pulse of seedlings coincident with a bumper acorn crop. One good acorn crop, however, coincident with proper site conditions may result in a single event of great

TABLE 2. RESULTS OF BACKWARD STEPWISE GENERAL LINEAR MODEL ANALYSIS ON THE DENSITY OF CALIFORNIA BLACK OAK SEEDLINGS (NUMBER/m<sup>2</sup>) AND VEGETATION ATTRIBUTES AT FOUR 21.1-HA STANDS IN PLACER COUNTY, CALIFORNIA. <sup>a</sup> Attributes log<sub>10</sub> transformed. <sup>b</sup> Attributes dropped from model if P-value > 0.05. Oak diameter was the covariate.

Attributes	Coefficient	SE	Std. coefficient	Tolerance	df	F	P-value	R <sup>2</sup>
Retained in model <sup>a</sup>								
Stand	—	—	—	0.59	3	11.48	0.000	0.40
Oak dbh <sup>b</sup>	0.46	0.17	0.25	0.89	1	7.53	0.008	
	Partial							
	Correla-							
	tions							
Dropped from model <sup>a</sup>								
Oak basal area <sup>b</sup>	0.09	—	—	0.63	1	0.67	0.415	
Conifer dbh <sup>b</sup>	-0.07	—	—	0.74	1	0.36	0.549	
Conifer trees <sup>b</sup>	-0.02	—	—	0.78	1	0.04	0.848	
Conifer height <sup>b</sup>	-0.01	—	—	0.85	1	0.00	0.960	
Analysis of Covariance								
	SS			MS	df	F	P-value	R <sup>2</sup>
Stand	3.37			1.13	3	15.46	0.000	0.41
Oak diameter <sup>c</sup>	0.70			0.70	1	9.55	0.003	
Error	7.50			0.07	103			

acorn germination and increase seedling densities. Acorn germination, however, is considered less significant as a recruitment source than sprouting by McDonald (1969, 1990) and McDonald and Tappeiner (1996), yet Savage (1994) expected seedlings to be a major source of recruitment of California black oak in the San Jacinto Mountains. Seedlings, rather than sprouts, appear to be the major recruitment source in the four study stands because approximately 70% of the mature oak trees sampled were single stems (Garrison et al. 2002).

Seedling densities increased with increasing oak

diameter ( $P < 0.001$ ) at all stands and increasing oak basal area at Stand 1 so diverse stand conditions with lesser and greater tree sizes and ages and basal areas should result in variable seedling densities. Larger diameter oaks have more wildlife habitat attributes such as dead branches, mistletoe (*Phoradendron villosum*), and acorns (Garrison et al. in press) so retaining large diameter trees is recommended where land management activities might affect these trees. Acorn production varies across California black oak diameters from 35–115 cm (Garrison et al. in press) but larger trees produce more acorns so retaining larger trees will maintain acorn crops and provide additional wildlife habitat benefits.

Stand 1 received a prescribed fire on 21 October 1981, while the other stands had not burned within the last two decades. This prescribed fire and the larger diameter oaks, flatter slope, and moderate oak overstory canopy cover were the most significant factors distinguishing Stand 1 from the other three stands and remains the most plausible reason why Stand 1 had more seedlings than the other stands. Prescribed fire appears to be a viable management tool in stands dominated by California black oak to promote seedlings and eliminate leaf litter (Anderson 1993) as well as to reduce threats from more severe, stand-replacing fires. Prescribed fires conducted in late fall or early spring with low to moderate fuel loads caused relatively low levels of mortality to California black oak seedlings and sprouts (Kauffman and Martin 1990), so prescribed fires can be timed to promote seedling establishment from acorns, maintain existing seedling and sapling numbers, and damage or kill competing vegetation. Fall burns conducted prior to the drop of acorns and deciduous leaves might be the best time to burn based on our limited data and lack of assessment

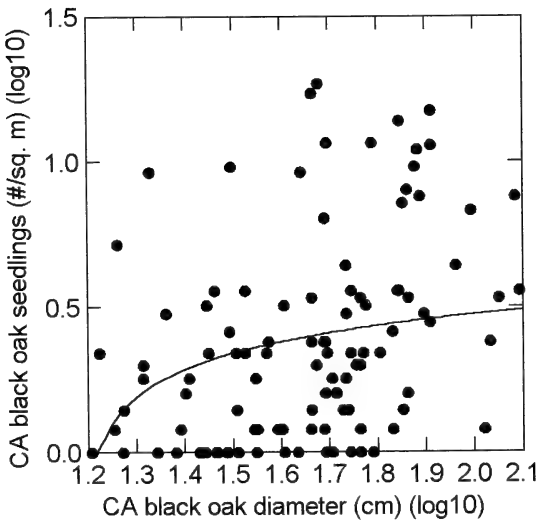


FIG. 2. Scatterplot of California black oak seedlings/m<sup>2</sup> and California black oak diameter (cm) from four 21.1-ha study stands measured in 1994 and 1995 in Placer County, California.

of the effects of prescribed fire on seedlings in our study area.

California black oak grows throughout its range in many different environmental conditions, and stands occur in even and uneven-aged conditions with varying amounts of conifers and other hardwoods (McDonald 1969, 1990; Garrison et al. 2002) so management objectives and actions will differ accordingly. Retaining acorn-producing trees while opening the canopy to moderate levels through thinning could produce conditions suitable for acorn germination and seedling growth. Thinning oak stands also improves acorn production (Healy 1997; Standiford et al. 2000). Finally, this study was done on a limited number of sites (four) in the central Sierra Nevada with mature California black oaks so these results may have limited application to stands with different vegetative attributes.

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CANOPY MACROLICHENS FROM FOUR FOREST STANDS IN THE  
SOUTHERN SIERRA MIXED CONIFER FORESTS OF  
SEQUOIA/KINGS CANYON NATIONAL PARK

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ABSTRACT

Canopy macrolichens were sampled using the “litter pickup” technique in four forest stands in the mixed conifer forests of Sequoia/Kings Canyon National Park. The purpose was to provide a basis for assessing lichen abundance trends in permanent forest plots, and to compare differences in lichen communities between four forest types typical of the southern Sierra Nevada. Each stand was characterized by a different conifer: sugar pine (*Pinus lambertiana* Dougl.), white fir (*Abies concolor* Gord. & Glend.), giant Sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). The standing crop of lichen litterfall was estimated at 33.6 kg/ha, 14.8 kg/ha, 6.9 kg/ha, and 7.6 kg/ha respectively. Seven macrolichens were present in the litterfall, in decreasing order of overall abundance: *Letharia vulpina* (L.) Hue, *Hypogymnia imshaugii* Krog, *L. columbiana* (Nutt.) J. W. Thomson, *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw. and *Melanelia exasperatula* (Nyl.) Essl., *M. subolivacea* (Nyl.) Essl., and *Lobaria* (Schreber) Hoffm. sp. A single factor ANOVA indicated that *L. vulpina* was equally distributed throughout the four stands, while *H. imshaugii* and *L. columbiana* were not. *H. imshaugii* was the most abundant lichen in the White Fir stand, although *L. vulpina* closely approximated it there. *L. vulpina* was most abundant in the Sugar Pine, Giant Sequoia and Jeffrey Pine stands, and all other lichens were much less abundant. A complex of factors explains the differences in lichen abundance; stand density, stand structure, and tree species composition appear most important, although site environmental conditions cannot be ruled out due to the lack of replication and small sample size in this study. The White Fir and Sugar Pine stands had 2–3 times the tree density as the Giant Sequoia and Jeffrey Pine stands. Giant sequoia and incense cedar (*Calocedrus decurrens* (Torr.) Florin) shed bark and therefore do not have abundant epiphytes on branches and tree boles. White fir appears to have a generally positive effect on lichen abundance, except in extremely dense stands. The abundance of *H. imshaugii* and *L. columbiana* were highly correlated with abundance of sugar pine. Although species diversity is low, standing crop of lichen litterfall is high, and may exceed many other forests in North America.

Key Words: Sierra Nevada, lichens, biomass, litterfall, canopy.

Macrolichens of forest canopies can be used to make inferences about a variety of ecosystem characteristics, including air quality, stand structure and history, stand age, and overall forest health (Segal and Nash 1983; Wetmore 1986; Boucher and Stone 1992; Bates and Farmer 1992; McCune 1993; Rhoades 1995). The distribution of these arboreal, non-crustose lichens across the landscape reflects the dynamic mosaic of environmental conditions (Hale 1974). Within the mixed-conifer forests of the southern Sierra Nevada Mountains in California, canopy macrolichens have received limited study.

The National Park Service and other government agencies are interested in determining whether the lichens are increasing or decreasing in abundance, because lichens may have value as indicators of environmental problems (McCune 2000). Smith (1980) did a taxonomic survey of the macrolichens in Sequoia/Kings Canyon National Park and found 40 species in 13 mostly forested study sites. An air

pollution impact survey of all the lichens of Sequoia/Kings Canyon National Park has identified 204 species (Wetmore 1986). Wetmore concluded that considering the dry climate, the lichen flora was diverse and healthy.

The purpose of this study was twofold: 1. To document the relative abundance of canopy macrolichens in four forest stands that are part of a permanent forest plot system in Sequoia/Kings Canyon National Park (Harmon et al. 1987; Riegel et al. 1988). These data provide a baseline for future sampling to determine temporal trends in canopy macrolichen abundance. 2. To compare the relative abundance of canopy macrolichens in four forest stands dominated by different species of conifers and representing different environmental conditions in the lower montane, mixed conifer forests of the southern Sierra Nevada Mountains.

The lower montane, mixed-conifer forests of the southern Sierra Nevada Mountains of California (1,600 m to 2,300 m) are characterized by giant



sequoia (*Sequoiadendron giganteum* (Lindl.) Buchh.) (Cupressaceae), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.) (Pinaceae), California red fir (*Abies magnifica* A. Murr.) (Pinaceae), sugar pine (*Pinus lambertiana* Dougl.) (Pinaceae), Jeffrey pine (*P. jeffreyi* Grev. & Balf.) (Pinaceae), and incense cedar (*Calocedrus decurrens* (Torr.) Florin) (Cupressaceae). Along a moisture gradient, giant sequoia occurs in mesic locations that do not dry out in the summer, white fir–mixed conifer (sugar pine and incense cedar) occurs in generally drier habitats, and Jeffrey pine occurs in the most xeric sites (Rundel et al. 1977; Vankat 1982). Fire and fire suppression play an extremely important role in stand composition and structure. In general, fire suppression results in an increase in the abundance of white fir (Rundel et al. 1977).

Appropriate sampling for canopy macrolichen studies can be challenging, particularly for studies of trends in abundance over time. Canopy access using tree climbing is the most direct means of sampling canopy macrolichens, but sampling tree crowns to determine stand level abundance (i.e. biomass) requires very large amounts of time in tall forests (Clement and Shaw 1999). As an alternative, McCune (1994) has developed a method to quantify the relative abundance of lichens in a forest stand by sampling litterfall. This “litter pick-up” technique allows one to estimate the mass of canopy macrolichens at the stand level, which can then be used to compare relative abundance to other stand types and to determine stand-level trends in abundance over time.

## METHODS

### Study Site/Reference Stands

The study site is located in the northwest portion of Sequoia National Park (Latitude 36°N and Longitude 118°W) (Fig. 1). We chose four of the six reference stands described by Riegel et al. (1988), each dominated by a different species of conifer; Jeffrey pine, white fir, sugar pine (mixed conifer), and giant Sequoia (in a riparian setting). The stands are between 2,012 and 2,219 m in elevation and representative of three vegetation types: Sierran mixed-conifer (sugar pine and white fir), giant Sequoia-mixed conifer (riparian), and Jeffrey pine (Riegel et al. 1988). The reference stands were established for long-term monitoring of vegetation and are cooperatively managed by the Sequoia/Kings Canyon National Park, Oregon State University, and the US Forest Service, Pacific Northwest Research Station (Acker et al. 1998). The reference stands were established in 1984 and re-measured in June of 1994. All trees >5 cm have been tagged and mapped, and each tree has the diameter at breast height measured. Information is collected on crown ratio, crown vigor, tree mortality and damage. All data presented on stand structure comes from the 1994 measurement.

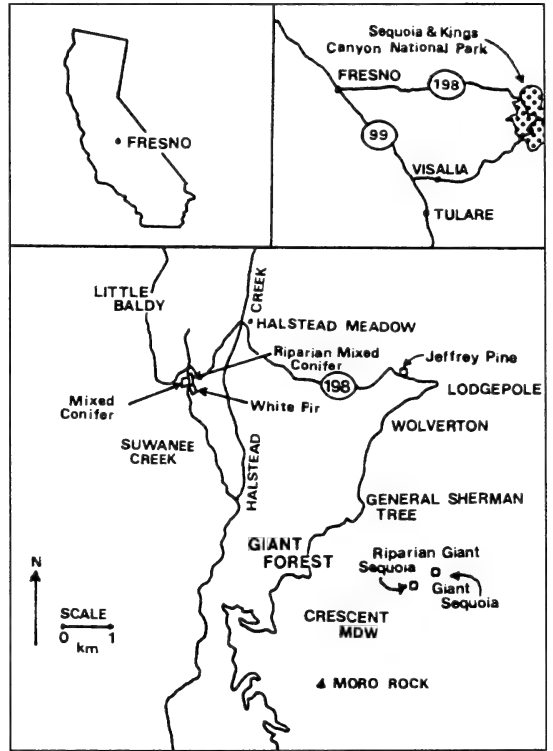


FIG. 1. Location of study site in Sequoia National Park, California (reproduced from Riegel et al. 1998). Four of these six reference stands were sampled, including White Fir, Jeffrey Pine, Riparian Giant Sequoia (Giant Sequoia) and Mixed Conifer (Sugar Pine).

The study site has a mediterranean climate, with cool, moist winters and hot dry summers. Precipitation averages 1172 mm/year (1932–1983 mean at Giant Forest/Lodgepole, Sequoia National Park) and falls mostly as snow between November and April. The hot dry summers have a strong influence on arboreal lichen communities, which are characterized by low species numbers and dominance by a few drought-tolerant species.

The Jeffrey Pine reference stand (1.0 ha) is on a moderately steep SE facing slope, (Table 1), with a glaciated granodiorite rock substrate. Exposed rock is common at the site. The canopy is open, dominated by Jeffrey pine (124 trees/ha), with California black oak (*Quercus kelloggii* Newb.) (Fagaceae) (60 trees/ha) (Table 2). Dense clumps of shrubs, especially green manzanita (*Arctostaphylos patula* Greene) (Ericaceae), are present. White fir (18 trees/ha), sugar pine (2 trees/ha) and incense cedar (5 trees/ha) occur in the lower plot where the slope flattens. This is a xeric, low productivity site. Jeffrey pine is adapted to the coarse textured soil found in the fissures of the glaciated granite (Riegel et al. 1988).

The White Fir reference stand (0.9 ha) is located

TABLE 1. SITE CHARACTERISTICS OF THE FOUR REFERENCE STANDS IN SEQUOIA NATIONAL PARK.

Reference stand	Stand size (ha)	Elevation (m)	Aspect	Topographic position	Average slope (%)
Sugar Pine	1.1	2091	southeast	midslope-bench	11
White Fir	0.9	2012	southwest	bench	20
Giant Sequoia	2.0	2219	southwest/southeast	lower slope	10
Jeffrey Pine	1.0	2109	southeast	upper slope	23

on a flat area above the east-side of Suwanee Creek (Table 1). There are scattered outcrops of bedrock in the stand. The stand has a dense canopy of white fir (420 trees/ha) and California red fir (33 trees/ha) near the stream which grades into a mixed-conifer forest with scattered sugar pine (56 trees/ha) and incense cedar (177 trees/ha) on the east side of the reference stand (Table 2). White fir is most abundant in all size- and canopy-classes, while incense cedar, sugar pine and California red fir are more abundant in the intermediate and suppressed canopy classes and smaller diameter-classes (Riegel et al. 1988).

The Sugar Pine reference stand (1.1 ha) is located to the west of Suwanee Creek approximately 200 m from the White Fir reference stand on a midslope bench (Table 1). The forest is a mosaic of large old sugar pine (110 trees/ha) and white fir (473 trees/ha) trees forming a relatively open canopy in the dominant (sugar pine 20 trees/ha, white fir 19 trees/ha) and codominant (sugar pine 11 trees/ha, white fir 42 trees/ha) canopy classes (Table 2, Riegel et al. 1988). There are clumps of suppressed white fir and incense cedar (78 trees/ha) interspersed throughout the stand where white fir dominates the smaller size and canopy classes. Cal-

ifornia black oak (16 trees/ha) and California red fir (7 trees/ha) are present in low numbers. The abundance of white fir in small size classes is thought to be a result of fire suppression (Riegel et al. 1988).

The Giant Sequoia reference stand (2.0 ha) is on a lower slope, and straddles both sides of Crescent Creek (Table 1). There is a narrow corridor of herbaceous vegetation along the creek. The stand has a typical mixed conifer over-story dominated by giant sequoia (24 trees/ha), which tower above the surrounding white fir (222 trees/ha) and California red fir (64 trees/ha) (Table 2). The true firs have a reverse J-shaped size distribution with a predominance of small stems, as is typical of shade tolerant species (Riegel et al. 1988).

Macrolichen Sampling

Canopy macrolichens were sampled on June 20–24, 1994 using 2-m radius (12.57 m<sup>2</sup>) litter pickup plots (McCune 1994). Litter refers to material (in this case lichens) fallen from the canopy. At fifteen randomly chosen grid points in each reference stand, a stake was placed in the center of the plot and a 2-m string was used to measure the radius of

TABLE 2. SPECIES COMPOSITION, NUMBER OF TREES PER HECTARE (TPH), TOTAL NUMBER OF SPECIES, DIAMETER (IN CM) CHARACTERISTICS, TREE SPECIES EVENNESS, TREE SPECIES RICHNESS BASED ON NUMBERS (KREBS 1989), TREE SPECIES RICHNESS BASED ON AREA (KREBS 1989) OF THE FOUR REFERENCE STANDS.

TPH by species	Stand			
	Sugar Pine	White Fir	Giant Sequoia	Jeffrey Pine
White Fir	472.6	420.5	221.5	18.0
Red Fir	7.1	33.0	63.5	0
Incense Cedar	77.9	177.3	0	5.0
Jeffery Pine	0	0	1.0	124.0
Sugar Pine	109.7	55.7	6.0	2.0
Ponderosa Pine	0	0	0	1.0
Cal. Black Oak	15.9	0	0	60.0
Giant Sequoia	0	0	23.5	0
TOTAL TPH	683.2	686.4	315.5	210.0
# Tree Species	5	4	5	6
median dbh	8.2	15.4	12.8	8.6
quad mean dbh	33.5	37.2	81.3	31.8
max dbh	154.1	148.7	600.0	133.1
Basal area (m <sup>2</sup> /ha)	60	74	164	17
Evenness	0.61	0.71	0.63	0.71
Rich No.	4.9 (0.27)	4.0 (0.00)	4.6 (0.51)	6.0 (0.00)
Rich Area	5.0 (0.00)	4.0 (0.00)	4.7 (0.47)	5.9 (0.35)

TABLE 3. TOTAL STANDING CROP OF CANOPY MACROLICHENS (kg/ha) ON THE FOREST FLOOR AND FREQUENCY OF OCCURRENCE IN 2 M RADIUS PLOTS. STANDARD DEVIATION IN PARENTHESES.

	Stand			
	Sugar Pine	White Fir	Giant Sequoia	Jeffrey Pine
Total Lichens				
Kg/ha	33.6 (27.7)	14.8 (18.5)	6.9 (12.9)	7.6 (16.5)
Frequency (%)	100	100	100	100
<i>Letharia vulpina</i>				
Kg/ha	15.04 (13.3)	6.5 (12.3)	4.8 (1.5)	7.35 (16.2)
Frequency (%)	100	73	93	100
<i>Letharia columbiana</i>				
Kg/ha	4.4 (5.4)	0.95 (1.3)	0.2 (0.4)	0.15 (0.18)
Frequency (%)	93	100	73	80
<i>Hypogymnia imshaugii</i>				
Kg/ha	14.1 (15.4)	7.3 (12.0)	1.8 (2.5)	0.08 (0.18)
Frequency (%)	93	93	80	33
<i>Bryoria fremontii</i>				
Kg/ha	0.01 (0.03)	0	0.08 (0.3)	0.01 (0.030)
Frequency (%)	20	0	20	13
<i>Melanelia</i> spp.				
Kg/ha	0	0	0.06 (0.1)	0
Frequency (%)	0	0	33	0

the plot. Flagging was located in four directions to denote the boundaries of the litter pickup plot. All fresh macrolichens (i.e., had not decayed beyond an identifiable state) were collected and placed in paper bags. Litter attached to wood was also collected, as was litter caught in shrubs up to 1 m off the ground that was not attached to the shrubs.

Macrolichens were transported to the lab, cleaned, and sorted to species. The lichens were then dried at 60°C for 24 hours and weighed. Lichen identifications were made using Hale and Cole (1988), and names follow Brodo et al. (2001). Species identifications were verified and unknown samples were identified by Bruce McCune, Oregon State University. Reference specimens are deposited in the University of Washington Herbarium.

Analysis

Biomass on each 2-m radius plot was transformed to g/ha for data analysis. The mean for the 15 plots in each reference stand was used to represent stand level abundance and reported as kg/ha with standard deviation. Total lichen biomass and biomass of *Letharia vulpina* (L.) Hue (Parmeliaceae), *L. columbiana* (Nutt.) J. W. Thomson (Parmeliaceae), and *Hypogymnia imshaugii* Krog (Parmeliaceae) were compared between reference stands using a single factor Analysis of Variance (Zar 1999), (d.f. = 3 between groups, and 56 d.f. within groups,  $\alpha = 0.05$ ).

Although the study included only four stands, we explored various descriptors of forest structure and composition as potential predictors of total lichen

litterfall biomass and biomass of each lichen species. Variation in lichen biomass was compared to variation in stand-level tree density and basal area, stem density of individual tree species, and tree species evenness and richness (from the rarefaction method (Krebs 1989)).

RESULTS

Species

Seven species were found in the macrolichen litterfall of these four reference stands: *Letharia columbiana*, *L. vulpina*, *Hypogymnia imshaugii*, *Bryoria fremontii* (Tuck.) Brodo & Hawksw. (Parmeliaceae), *Melanelia exasperatula* (Nyl.) Essl. (Parmeliaceae), and *M. subolivacea* (Nyl.) Essl. (Parmeliaceae) and a *Lobaria* (Schreber) Hoffm. (Lobariaceae) sp. fragment. The *Lobaria* fragment was unidentifiable to species, and is not discussed further. The *Letharia* species and *H. imshaugii* were present in all four stands, while *Bryoria fremontii* was absent from the White Fir stand. The two *Melanelia* species were present only in the Giant Sequoia stand which at six species, had the highest macrolichen litterfall species diversity. The other stands had four species, including the *Lobaria* sp. fragment at the White fir stand.

Abundance

The Sugar Pine stand had the highest standing crop of lichen litterfall (33.6 kg/ha) (Table 3). The White Fir stand had about ½ as much (14.8 kg/ha) and the Giant Sequoia (6.9 kg/ha) and Jeffrey Pine

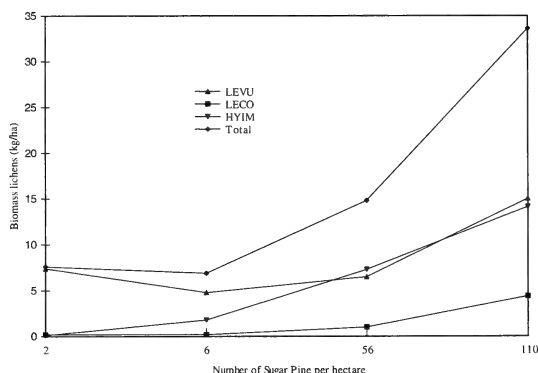


FIG. 2. Density of Sugar Pine per hectare on the four reference stands versus the standing crop of litterfall lichen biomass per hectare for total lichens, *Letharia vulpina* (LEVU), *L. columbiana* (LECO), and *H. imshaugii* (HYIM). Sugar Pine density corresponds to forest stands: 2 = Jeffrey Pine, 6 = Giant Sequoia, 56 = White Fir, 110 = Sugar Pine.

(7.6 kg/ha) stands had about one fourth that much lichen litterfall biomass as the Sugar Pine stand. In three of the four reference stands, lichen litterfall biomass was dominated by a combination of *L. vulpina* and *H. imshaugii*. In the Giant Sequoia, White Fir, and Sugar Pine stands, *L. vulpina* accounted for 44% to 70% of lichen litterfall biomass and *H. imshaugii* accounted for 25% to 49%. The Jeffrey Pine stand was unusual in that nearly all the lichen litterfall biomass (97%) was contributed by a single species, *L. vulpina*. The only other species to account for 10% or more of the lichen litterfall biomass of any stand was *L. columbiana*, which was 13% of the biomass for the Sugar Pine stand.

The ANOVA indicated significant differences between reference stands in biomass of total lichens ( $P < 0.01$ ), *L. columbiana* ( $P < 0.01$ ), and *H. imshaugii* ( $P < 0.01$ ). No significant difference was found for *L. vulpina* ( $P = 0.16$ ). Biomass of *L. columbiana* and *H. imshaugii* generally increase with increasing density of sugar pine (Fig. 2). Tree density, basal area, tree species evenness, tree species richness based on numbers, or tree species richness based on area (Table 2, 3) shows little relationship to the variation in total biomass of lichens.

## DISCUSSION

### Species Richness and Distribution

The lichen litter pick-up technique documented only seven species of lichens in these four forest stands. This is low species diversity, even for dry habitats. Smith (1980) found 40 species of macrolichens in the Ash Mountain to Grant Grove (Highway 198) region of Sequoia-Kings Canyon National Park and also included Cedar Grove. He sampled

13 sites using a floristic survey method that included all substrates, not just canopy lichens. The litter pick-up technique is not a 'stand-alone' method for surveys of species diversity, because species capture is low. The technique is best used in conjunction with other survey techniques that specifically search for different species of lichens (McCune and Lesica 1992; McCune 1994). However, it is a good technique for determining the relative abundance of the predominant forest canopy species. This is important for monitoring change in lichen communities.

In a study of lichens on conifers and their relation to air pollution in the Southern California mountains outside of Los Angeles, Sigal and Nash (1983) reported 16 species, the same number reported by Hasse for the same area in 1913 (in Sigal and Nash 1983). The lichen flora showed a strong relationship to air pollution: only eight of the original 16 species reported by Hasse were present in the most heavily polluted forests of the San Bernardino and San Gabriel Mountains. Sigal and Nash (1983) also rated the sensitivity of lichen species to air pollution, including several species we observed. They ranked *L. vulpina* as tolerant, *M. subolivacea* as moderately tolerant, and *B. fremontii* as very sensitive.

Smith (1980) has given species accounts of all 40 species he observed in Sequoia/Kings Canyon National Park, including the six species observed in this study. According to Smith, *Bryoria fremontii* is uncommon, and was only collected once from the bark and branches of *Pinus murrayana* (Sierra lodgepole pine, *P. contorta* subsp. *murrayana* (Balfour) Engelman (Pinaceae)) in the Stony Creek area. We found *B. fremontii* in the Jeffrey Pine, Giant Sequoia, and Sugar Pine reference stands. *Hypogymnia imshaugii* was uncommon and was collected on *A. concolor* in the Crystal Cave Junction area. Smith found *H. enteromorpha* (Ach.) Nyl. (Parmeliaceae) to be common and sometimes very abundant in all areas above 450 m. This in contrast to our finding of *H. imshaugii* in all four sites, and a lack of collections for *H. enteromorpha*. Hale and Cole (1988) note that in the past, virtually all fertile Hypogymnias in California were called *H. enteromorpha*, but that this name is now limited to populations along the coast that are characterized by grossly inflated branches, and that this species does not occur in the Sierra Nevada. Hale and Cole (1988) also indicate that *H. imshaugii* is very common in Sequoia National Park.

Smith considers *Letharia columbiana* and *L. vulpina* to be two of the most common and abundant lichens in the park between 1200 m to 2700 m elevation. He found them growing on numerous tree species all through the study region. We also found these two lichens to be abundant. Interestingly, *L. vulpina* was the more abundant of the two species with 3 to 10 times the biomass of *L. columbiana* in the reference stands. Smith found *Melanelia subo-*

*livacea* (called *Parmelia subolivacea* Nyl.) abundant in all 13 study sites and in some trees the upper branches were completely covered by the lichen. It was present on a wide variety of conifers and hardwoods. *Parmelia exasperata* De Not. was described as commonly found on *Quercus*, widespread in the Ash Mountain area, Potwisha, Buckey Flats and Deer Ridge. This may be what we identified as *M. exasperatula*. We found these two species were present only in litterfall of the Giant Sequoia reference stand.

### Abundance

*Letharia vulpina* was the dominant lichen in three of these forest stands, and was generally equally distributed throughout the four forest stands. *L. columbiana* and *H. imshaugii* were not equally distributed and showed strong patterns of increase with increasing sugar pine and white fir. The extreme xeric conditions of the Jeffery Pine stand may have a negative influence on *L. columbiana* and *H. imshaugii*.

McCune (1994) has investigated canopy litterfall relationships in the Pacific Northwest of North America. He found that the ratio 1:100 (litter: canopy lichens) was fairly consistent in Douglas-fir forests for late summer standing crop of lichen litter. Thus about 100 times the amount of lichen found on the forest floor in late summer will be in the canopy. This relationship has not been tested for forests of the Sierra Nevada. However if it is valid for the Sierra Nevada, the canopy biomass of macrolichens in the four reference stands would range from 0.7 Mg/ha in the Giant Sequoia stand to 3.4 Mg/ha in the Sugar Pine stand, with intermediate values for the Jeffery Pine and White Fir stands (0.8 Mg/ha and 1.5 Mg/ha, respectively). These numbers are surprisingly large, perhaps in part because litter was collected in June rather than late summer. Typically a large pulse of lichen litter from winter storms will gradually disappear over the next 6–12 months depending on the species (McCune and Daley 1994). Another possibility is that the mildly toxic *Letharia* spp are resistant to herbivory, resulting in greater persistence on the forest floor.

Some of the most productive old-growth Douglas-fir stands in the Pacific Northwest have 1.3 to 1.9 Mg/ha of macrolichens in the canopy (McCune 1993; McCune et al. 1997). Boucher and Nash (1990) estimated 0.75 Mg/ha macrolichens for canopies of Blue Oak in California (36°N Latitude) while Turner and Singer (1976) estimated 1.9 Mg/ha for a Pacific Silver Fir stand in the western Cascades of Washington. For further information on the biomass of epiphytes see Boucher and Stone (1992) and Rhoades (1995). The relationship of lichen litter biomass to lichen biomass in the canopies of Sierra Nevada forests is a key area for future research.

### Factors Influencing Lichen Abundance

Lichen species composition and abundance in forest canopies is influenced by a multitude of factors. Among other things, this includes tree species, bark texture/chemistry, stand age, ecological continuity of the forest (Bates and Farmer 1992), tree density, forest structure, disturbance history, air pollution, climatic conditions, and forest management practices (Hale 1974; McCune 1993; Rhoades 1995). Within the southern Sierran mixed-conifer forests that we sampled, the most obvious influences on lichen species composition and abundance include tree species composition, stand density, and forest stand structure. It should be stressed that the generality of our interpretation is limited by the small sample size and no replication of stand types.

Differences in tree density did not directly correspond to differences in lichen biomass as stands with similar tree density differed in lichen biomass by a factor of 2 (Sugar Pine and White Fir) and stands with similar lichen biomass differed in tree density by 50% (Giant Sequoia and Jeffrey Pine). Tree species composition may explain some of these differences. Though they were similar in density, the Sugar Pine and White Fir stands were very different in stand structure and species composition. The White Fir stand was uniform in stand structure creating more evenly shaded tree boles, and had over twice as many incense cedar (78/ha in the Sugar Pine to 177/ha in the White Fir stand). Incense Cedar has exfoliating bark that sheds lichens. The Sugar Pine stand was more open with twice the number of sugar pine trees (110/ha in sugar pine to 56/ha in the fir stand) and a complement of dominant and codominant trees in the overstory, which provides for more sunlight on tree boles and branches. Thus, the Sugar Pine stand may have had an optimal combination of tree species composition and stand structure to provide for abundant lichen biomass.

Giant Sequoia represented 74% of the basal area and 80% of the stand wood volume in the Giant Sequoia stand although accounting for only 7% of the stems. Giant sequoia also has exfoliating bark, hence the lichens are rare on the tree bole, and only abundant on dead wood and cones (Steve Sillett and Joel Clement, personal communication). This might explain why the Giant Sequoia and Jeffrey Pine stands were similar in lichen litterfall biomass even though the sequoia stand had 50% more trees. The Jeffrey Pine stand approached a woodland setting, with widely scattered trees, among outcrops of rock. *Letharia vulpina* was the dominant lichen in this forest, perhaps showing a tolerance for xeric conditions and compatibility for Jeffrey pine bark texture and chemistry.

The physical settings of the forest plots, such as aspect and proximity to streams, may also play a role in lichen abundance. The Giant Sequoia stand

had a stream running through it, the White Fir stand and Sugar Pine stands were adjacent a stream, and the Jeffrey Pine stand was not influenced by a stream. A xeric to mesic environmental gradient was not measured in a systematic and replicated way in this study, and therefore conclusions regarding the overall effect of tree species composition as the major influencing factor associated with lichen abundance should be taken as a hypothesis needing further study.

### CONCLUSIONS

We observed low species diversity of canopy lichens in the mixed-conifer forests of the southern Sierra Nevada Mountains, yet an unusually high stand biomass of lichen litterfall. The Sugar Pine stand would be one of the highest biomass estimates for lichens in North America if the 1:100 ratio of litterfall to canopy lichen biomass for Northwestern forests (McCune 1994) holds true in Sierran forests. The early summer sample period and possibility of longer persistence on the forest floor by *Letharia* spp. may explain these higher numbers. Tree species composition (especially abundance of sugar pine), and canopy openness/vertical structure appear to play a role in the abundance of canopy macrolichens, although the lack of replication within stand types and along the environmental moisture gradient preclude a definitive analysis. Characteristics of forest stands are controlled by a complex of factors, but in the future, anthropogenic influences such as fire suppression and controlled burning, air pollution, and climate change may become very important in determining lichen abundance. Long-term monitoring of lichens is important for understanding their role in the dynamics of ecosystems and how they will respond to anthropogenic influences.

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*CALYSTEGIA SILVATICA* (CONVOLVULACEAE) IN WESTERN  
NORTH AMERICA

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At the kind request of the Jepson Manual editor, I contributed the account of *Calystegia* to the recent edition of the Jepson Manual (Brummitt in Hickman 1993: 517–521) despite my never having set foot in California at the time. My knowledge of the taxa in California, where half the genus is endemic, was based entirely on extensive study of herbarium specimens sent on loan from the major herbaria in the late 1960s. I was unaware of any introduced species established in the state, though I was familiar with several species of the genus which had become very well naturalized as weeds in various other parts of the world.

In 1997 I attended a meeting at the California Academy of Sciences, and, to my great delight, was able to see in the field for the first time many of the *Calystegia* taxa native to the state. But, to my surprise, I was able to add one introduced species to the Californian list before ever stepping into the field, when I reidentified a specimen in the CAS collections as *C. silvatica* (Kit.) Griseb., native of southern Europe. The specimen was collected at Stinson Beach in Marin Co. in the late 1950s by J.T. Howell and then identified and laid away as *C. sepium* (L.) R.Br. My host at CAS, Tom Daniel, immediately agreed to take me to Stinson Beach to see if the plant was still there, and, sure enough, it was there in great abundance on waste ground over a distance of perhaps 100 m, swamping other vegetation and climbing to a height of 3 m, very conspicuous even to a passing motorist. It was surprising that such a conspicuous plant has been so overlooked, and we collected additional material: Marin Co., Stinson Beach, roadside in town, alt. 20 m, 122°39'W, 37°54'N, abundant, rampant over vegetation to 3 m, 31 May 1997, *R.K. Brummitt & T.F. Daniel* 19614 (CAS, K, MO, RSA, UC).

Alerted to the presence of this species in the area, I noticed it again a few days later some 11 km east of Stinson Beach on waste ground in the town of Mill Valley, and collected it again: Marin Co., Mill Valley, near foot of Reed Street, roadside in suburban area, 122°33'W, 37°54'N, climbing over bushes and roadside vegetation to 3 m, 10 June 1997, *R.K. Brummitt* 19672 (CAS, K). Again, the strongly climbing stems and the large white flowers were very conspicuous.

*C. silvatica* is readily distinguished from any *Calystegia* in northern or mid California by its very vigorous habit, large glossy leaves, and particularly its large flowers (corolla 50–75 mm) with two large

bracteoles at the base which are inflated and overlapping and more or less obscuring the calyx. In southern California it is approached in its flowers and bracteoles by *C. macrostegia* (House) Brummitt subsp. *macrostegia* and subsp. *amplissima* Brummitt from the Channel Islands, but that species is woody at the base whereas *C. silvatica* is rhizomatous, and the two species are almost certainly not closely related despite their superficial similarity.

The pan-temperate complex of *C. sepium* and related species, including *C. silvatica*, is difficult to resolve taxonomically, consisting of a series of geographical taxa with minor distinguishing characters. My concept of *C. silvatica* includes plants native of eastern N. America, southern Europe and as far east as Iran, and China, which occur sympatrically with *C. sepium* except in China and are distinguished from it by their large inflated and overlapping bracteoles. Those from eastern N. America and China are characterised by sometimes having twin peduncles in leaf axils and a rather square leaf sinus, and I refer them to subsp. *fraterniflora* (Mack. & Bush) Brummitt. In the Mediterranean region those from central and southern Italy eastwards have a longer range of flower size and bigger, more inflated bracteoles with a rounded to emarginate apex, and these are referred to subsp. *silvatica*. Plants from northern Italy and southern Switzerland westward to Spain tend to have a smaller range of flower size and an obtuse apex to the bracteoles. Despite more than thirty years of hesitation over whether to give this variation formal taxonomic recognition—which necessitated a lengthy note on the matter in *Flora Europaea* (Brummitt 1972) instead—I have recently formally separated these southwestern European plants as subsp. *disjuncta* Brummitt (see below).

Both of the Mediterranean subspecies were introduced into the British Isles about a century ago, probably as garden ornamentals, and both are now serious weeds there (but, curiously, not so in other north European countries). Subsp. *silvatica* is also known as a weed in Australia, where subsp. *disjuncta* appears not to have been introduced. In North America, however, it seems to have been only subsp. *disjuncta* that has become established, this being known from specimens collected in Washington State from 1927 onwards and also from British Columbia and Oregon. Its occurrence in California is thus not very surprising. Subsp. *fra-*



*terniflora* has been recorded as a rare alien in the British Isles, almost certainly introduced from North America, but has not become established.

In the standard text on the plants of the Pacific Northwest, Hitchcock (1959) included all these taxa in *Convolvulus sepium* L. The plant figured there under this name on p. 88 is very probably *C. silvatica* subsp. *disjuncta*. The plant referred to in the text as var. *fraterniflorus* is probably also this taxon and this epithet is misapplied here. The statement that it is native of the eastern United States is incorrect. It was already described by Hitchcock here as a difficult weed.

All taxa in the *C. sepium* complex spread vigorously by rhizomes and tend to become aggressive weeds, often swamping the vegetation the stems climb over. The rhizomes are, however, not quite so deep-rooted as those of *Convolvulus arvensis* L., a major weed in California, and they are not quite such a persistent pest. Seed dispersal in *C. sepium* and allies is less significant than vegetative spread, since there is no obvious dispersal mechanism and the seeds tend to merely fall to earth beneath the parent plant. Furthermore, all plants in this complex are self-sterile and single populations normally do not set seed at all. *C. silvatica* tends to be more vigorous in its vegetative spread than the variants of *C. sepium* are, and its potential as a serious weed is considerable. It seems that in Britain new populations may be established by accidental transport of pieces of rhizome (see, for example, notes in Brummitt & Chater 2000).

***Calystegia silvatica*** (Kit.) Griseb., Spic. Fl. Rum. 2: 74 (1844) subsp. ***disjuncta*** Brummitt in *Lagascalia* 18: 339 (1996).

Additional specimens documenting known range in North America.

BRITISH COLUMBIA. West Vancouver, 16 Ma-

rine Drive, roadside, 6 July 1955, *W. Bird* 1239 (BM); Vancouver, Bush Crown & 25 Ave., 5 May, 1956, *W. Bird* 2008 (BM); Vancouver, Canoe Pass Delta, bank between road and river, 1 Sept. 1957, *W. Bird* 3533 (BM).

WASHINGTON. Marysville, fields, July 1927, *J.M. Grant* (US); Bank of R. Spokane, July 1931, *Sister M. Milburge* (WTU); Seattle, end of Green Lake, dumping ground, 28 July 1933, *J.W. Thompson* 9619 (NY); Port Blakely, in thicket, 17 June 1934, *W.J. Eyerdam* (L, MO); Whatcom Co., Birch Bay, 19 July 1937, *W.C. Muenscher* 8343 (DAO); King Co., Fort Lawton, roadside hedges, 25 July 1937, *W.J. Eyerdam* (F, MO); ½ mile NE of Seattle, near Sand Point, in thicket, 10 June 1949, *W.J. Eyerdam* (BM); Shelton—Woodsport road, moist sandy soil, 30 July 1950, *P.E. Freer* 320 (WTU).

OREGON. Just east of Corvallis, across Van Buren St. bridge, 15 June 1960, *L.R.J. Dennis* 2227 & *G. van Vechten* (NY).

It is a pleasure to thank many botanists we have assisted me in the field in California on my three visits to look at *Calystegia* in 1997, 1998 and 1999, especially Barbara Ertter (Berkeley) and Tom Daniel (California Academy of Sciences).

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## NOTEWORTHY COLLECTIONS

### ARIZONA

*MANCOA PUBENS* (A. Gray) Rollins (BRASSICACEAE).—Cochise County, San Pedro Riparian National Conservation Area, Kolbe site ca. 2 km SW of San Pedro Inn Bed and Breakfast, ca. 3 km S of Hereford Bridge, ca. 100 m E of San Pedro River. N31°24.961' W110°6.227', elevation 1274 m, June 6, 2001. Found in sacaton grassland habitat with young mesquite; upper flood plain in sandy-loamy soil; level, open aspect. Associated species include *Sporobolus wrightii*, *Prosopis velutina*, *Erigeron concinnus*, *Xanthocephalum gymnospermoides*, *Helenium thurberi*, *Conyza coulteri*, *Conyza canadensis*, *Plantago* sp., *Salix goodingii*, Elizabeth Makings 365 (ASU).

*Previous knowledge.* West Texas to Coahuila, Mexico (Rollins, The Cruciferae of Continental North America, Stanford University Press, 1993). Other regional collections: Hinckley s.n. (ARIZ) Jefferson Davis County, Texas in 1937; Waterfall s.n. (ARIZ) Jefferson Davis County, Texas in 1943; Andres Rodriguez 861 (TEX) Coahuila, Mexico in 1983; four collections from Jefferson Davis County, Texas (TEX); two collections from Presidio County, Texas (TEX); and four collections from Brewster County, Texas (TEX).

*Significance.* First record for the species in Arizona. This collection is approximately 500 km from nearest known collections in Jefferson Davis County, Texas. This was an isolated annual/biennial, inconspicuous in its in sacaton grassland community, which may explain why it has been under collected. This habitat is widely recognized as a major corridor for migratory birds. Seed size make wind dispersal unlikely, therefore, bird dispersal may explain the considerable range extension for this species.

—ELIZABETH MAKINGS, Department of Plant Biology, Arizona State University, P.O. Box 871601, Tempe, AZ 85287-1601.

### WASHINGTON

*BACCHARIS PILULARIS* DC (ASTERACEAE).—Pacific Co: Fort Canby State Park, Beard's Hollow. R11W, T10N, S23, SW ¼ of NE ¼, USGS 7.5 minute "Cape Disappointment" quad, 30 m SW of Beard's Hollow overlook on State Route 100, 1.5 km W of Ilwaco. Growing on SW facing cliffs in low coastal seacleft meadows above dune forest, with *Poa unilateralis*, *Festuca rubra*, *Sedum oregonensis*, *Vulpia bromoides*, and below *Calamagrostis nutkaensis* meadows. Colony of 30–50 upright plants, 0.5–2 m tall, at 10–30 m elevation. One plant grows on sand 100 m to the north, at an elevation of 4 m, with *Alnus rubra*, *Ammophila arenaria*, *Leymus mollis*. First seen in 1981, revisited and collected while in flower on 9-15-2001. K. Sayce (WS, OSC, WTU).

*Previous knowledge.* *Baccharis pilularis* occurs from Oregon to northern Mexico on coastal bluffs to oak woodlands, occasionally on serpentine, 0–750 (1500) m. The nearest known occurrences are Gearhart and Cannon Beach, Clatsop County, Oregon (information supplied by

Richard Halse, OSU Herbarium, Corvallis). *Baccharis pilularis* is increasingly common to the south, and is a member of shrub communities, including chaparral and coastal sage, in California.

*Significance.* This is the northernmost known location and only Washington site for *Baccharis pilularis*, and is 30 km north of the next known site in Oregon. This small population may represent remnants of a species that was more widespread in warmer climates.

—KATHLEEN SAYCE, P.O. Box 91, Nahcotta WA 98637. kas@sbpac.com

### MOOREA, SOCIETY ISLANDS, FRENCH POLYNESIA

*ARUNDO DONAX* L. (POACEAE).—Poa Poa, University of California, Gump Biological Research Station, hillside grounds of main house and beyond, 17°30'S, 149°49'W, elev. 100 m, 25 October 2000, Mitchel P. McClaran and James W. Bartolome 00-04 (ARIZ, UC).

*Previous knowledge.* Native to Mediterranean (Allred 1993, In: Hickman (ed.), The Jepson Manual, University of California Press, Berkeley, CA, p. 1235) cultivated worldwide, and regularly naturalized. Known from nearby Huahine and Raiatea islands (Welsh 1998, Flora Societensis, Electronic PrePrint Services Inc., Orem, UT).

*Significance.* First record of this non-native species for Moorea. Several large plants spreading from landscape grounds to wild hillside. Based on evidence from Southern California, this species spreads via vegetative reproduction, can dominate riparian vegetation through competitive exclusion, and can facilitate an increase in fire occurrence (Bell 1997, In: Brock et al. (eds.). Plant Invasions: Studies from North America and Europe. Backhuys Publishers, Leiden, Netherlands, p. 103–113).

*CHLORIS BARBATA* Sw. (POACEAE).—Poa Poa, in waste area surrounding Supermarche Aré market, 17°29'S, 149°49'W, elev. 2 m, 23 October 2000, Mitchel P. McClaran and James W. Bartolome 00-01 (ARIZ, BISH, UC).

*Previous knowledge.* Native to New World tropics and naturalized worldwide, and known from nearby Tahiti and Raiatea islands (Welsh 1998).

*Significance.* First record of this non-native species for Moorea. Naturalized and common along roadsides and other waste areas near human settlements. This distribution is consistent with observations from other South Pacific archipelagoes, including Hawaii, Samoa, Tonga, Fiji, Guam, and Belau (Whistler 1995, Wayside Plants of the Islands, Isle Botanica, Honolulu, HI).

*HYPARRHENIA RUFA* (Nees) Stapf (POACEAE).—ca. 2 km S of Afariatu, near and in abandoned livestock pasture, assoc. with *Setaria sphacelata* (Schumach.) Stapf & C.E. Hubb. ex. M.B. Moss, 17°34'S, 149°47'W, elev. 4 m, 24 October 2000, Mitchel P. McClaran and James W. Bartolome 00-02 (ARIZ, BISH, UC).

*Previous knowledge.* Native to tropical Africa and America (Renvoize 1984, The Grasses of Bahia, Kew Botanical Garden, England). Known from nearby Tahiti and Raiatea islands (Welsh 1998).

**Significance.** First record of this non-native species for Moorea. Not common, but plants present beyond boundaries of area seeded for livestock pasture. Naturalized, and likely to continue to spread based on experience in Australia, Hawaii, and Venezuela. Considered a weed in Australia because it spreads from seeded areas into native vegetation (Lonsdale 1994, *Australian Journal of Ecology* 19: 345–354). Spread increases the occurrence of fire, which hastens its increase and the decrease of native species in Hawaii and Venezuela (Smith and Tunison 1992, In: Stone et al. (eds.), *Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research*, University of Hawaii Cooperative National Park Resources Study Unit, Honolulu, HI, p. 394–408, and Baruch 1996, In: Solbrig et al. (eds.), *Biodiversity and Savanna Ecosystem Processes: A Global Perspective*, Springer-Verlag, New York, NY, p. 79–93), although it will spread and dominate native vegetation in the absence of fire and grazing (San Jose and Farinas 1991, *Acta Oecologia* 12:237–247).

*SETARIA SPHACELATA* (Schumach.) Stapf & C.E. Hubb. ex. M.B. Moss (POACEAE).—ca. 2 km S of Afariatu, near and in abandoned livestock pasture, assoc. with *Hyparrhenia rufa* (Nees) Stapf, 17°34'S, 149°47'W, elev. 4 m, 24 October 2000, Mitchel P. McClaran and James W. Bartolome 00-03 (ARIZ, BISH, UC).

**Previous knowledge.** Native to tropical and subtropical Africa, and Yemen (Hacker 1992, In: 't Mannetje & Jones (eds.), *Plant Resources of South-east Asia*, No. 4, Pudoc Sci. Publ., Wageningen, Netherlands, p. 201–203). Known from seeded pasture, Taiaapu Plateau on nearby Tahiti island (Welsh 1998).

**Significance.** First record of this non-native species for Moorea. Not common, but plants present beyond boundaries of area seeded for livestock pasture. Possibly less likely to spread from seeded area than *Hyparrhenia rufa* based on its absence from Australian weed lists (Lonsdale 1994). However, that prediction may be incorrect because this collection is apparently the more fecund cultivar 'Splenda', based on intermediate values for some characters (number of culm nodes, culm diam., lf width, and panicle length) between vars. *sericea* and *splendida* (Hacker 1992). This cultivar, developed in Australia in the 1980s, had high yields in Southeast Asian and Southern Pacific trials, and unlike the two varieties, will produce fertile seeds in abundance (Hacker 1992).

—MITCHEL P. MCCLARAN, School of Renewable Natural Resources, 325 Bioscience East, University of Arizona, Tucson, AZ 85721 and James W. Bartolome, Department of Environmental Science, Policy, and Management, 145 Mulford Hall, University of California, Berkeley, CA 94720.

## REVIEW

*Seeing things whole: the essential John Wesley Powell*. Edited by WILLIAM DEBUYS. 2001. Island Press, Covelo, CA. 388 pp. \$27.95. ISBN 1-55963-872-9.

Guessing right about the direction history will take is always a doubtful proposition, but as William deBuys makes clear in *Seeing things whole: the essential John Wesley Powell*, the famous one-armed explorer and scientist did guess right about enough important issues of his time to still be worth reading today.

Actually, as deBuys makes clear, to say that Powell "guessed right" is not to do him the justice he deserves. A true polymath, Powell spent decades studying the landscape and peoples of the region he cared about—the American West. First as explorer of the Grant Canyon, and then, over time, as geologist, ethnologist, bureau administrator, social planner, public figure, and philosopher, Powell worked over the same territory again and again from endlessly evolving perspectives, seeing patterns where his contemporaries clearly did not.

Powell has not been ignored by the historians of recent times, and it is a tribute to the Major's significance that he has been the subject of biographies by both Wallace Stegner and Donald Worster. What deBuys adds to these two excellent histories is Powell in his own words. This selection of Powell's

writings varies from excerpts from his well-known Colorado River writings, to things much less known including such forgotten statements as the Major's address to Montana's 1889 constitutional convention. Particularly welcome are several chapters from Powell's often quoted (but not so often read) *Report on the arid lands*.

What deBuys shows us is not a Powell who escaped all the constraints of his times, but rather a powerful and original thinker who worked hard to see what was going on in his time. Certainly, by contemporary standards, Powell could not escape 19th century expectations that the native people of North America were destined to disappear, and as an ecologist he had trouble (as many still do) coming to grips with the role of the fire in the West, but what deBuys shows clearly is that in a number of critical areas Powell did break through into new ways of thinking about a number of still critical issues. Certainly, his recognition that the nation's land laws would victimize both many of those who tried to settle the West and the land itself, was unprecedented and still highly valid today. William deBuys is to be thanked for bringing a useful selection of Powell's original writings back into easy reach.

—WILLIAM TWEED. Sequoia-Kings Canyon National Parks, Three Rivers, CA 93271.

## REVIEW

*Inventory of rare and endangered plants of California*, sixth edition. California Native Plant Society, Rare Plant Scientific Advisory Committee, David P. Tibor, convening editor. 2001. California Native Plant Society, Sacramento, CA. 388 pp. Softcover \$29.95. ISBN 0-943460-40-9.

The California Native Plant Society's recent publication of the sixth edition of the *Inventory of rare and endangered plants of California* offers a welcome update on the constantly changing condition of endangered plants and habitats. Plants species' rare, threatened or endangered status has expanded by a hefty 19% since the fifth edition, issued in 1994, so it is an essential addition to any library.

This version basically adheres to the same successful formula of its predecessors. However, some new features that appear in this *Inventory* are the inclusion of rare, non-vascular bryophytes (mosses, liverworts and hornworts), each species' typical elevation ranges, county indexing for all 2073 plants, and a new common name appendix. Inside covers have helpful lists of often-used, and too-often forgotten acronyms.

The *Inventory* is a massive collaborative effort utilizing the talents of hundreds of scientific contributors who have spent untold hours in the field identifying, mapping, and gathering botanical data to be added to or updated in the Department of Fish and Game database. The importance of this work has its basis in that critical and balanced scientific input. But with a readership as diverse as developers, biological consultants, educators and private

landowners, the *Inventory* also must and does adeptly make this information understandable and available to all intellectual levels, thereby providing the greatest opportunity for early detection as well as avoidance of potential environmental conflicts.

Introductory chapters espouse both CNPS policies as well as those of various state & federal agencies—simplifying and clarifying the sometimes overwhelming mass of plant protection guidelines and legislations. Peggy Fiedler again provides the scientific rationale for the plant endangerment rating system.

The actual 'Threatened and Endangered Plant Inventory' is alphabetically organized by scientific name for easy access. In most cases, specific entries contain the following information: scientific names as well as family and common names, associated authorities, CNPS' rarity rating (and those given state and Federal status as well), occurrences by county with map coordinates, key identifying characteristics, typical habitat and pertinent historical notations with literary referencing.

The *Inventory of rare and endangered plants* is one of the most tangible and fruitful of CNPS' many pursuits. Convening Editor Tibor and his legions of collaborators have not only achieved their intent for the *Inventory*, which encourages "... conservation planning and enforcement of environmental laws that protect rare species," they have ably furthered the goals of the California Native Plant Society.

—MELANIE BAER-KEELEY. Division of Resources Management, Branch of Vegetation Management, Sequoia Kings Canyon National Park, Three Rivers, CA 93271.

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- Oct. 17     Truman Young, Dept. of Environmental Horticulture, UC Davis  
Ecological restoration: an emerging conservation strategy.
- Nov. 21     Randy Jackson, ESPM, UC Berkeley  
Spring-fed wetland structure and function in California oak savannas.
- Jan. 16     David Ackerly, Dept. of Biological Sciences, Stanford University  
Fire, drought, and the evolution of chaparral shrubs.
- Feb. 15     Annual banquet (University of San Diego)**  
**Jon Rebman, San Diego Natural History Museum**  
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- Mar. 20     Kim Steiner, California Academy of Sciences  
The evolution of a specialized pollinator system in southern Africa.
- April 17     Todd Dawson, Dept. of Integrative Biology, UC Berkeley  
Giants in the mist: coastal redwoods and the land-sea interface.
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### ABSTRACT

*Crupina vulgaris*, with populations in Sonoma and Modoc counties, is a relatively recent Mediterranean invader among the 1045 alien plant species naturalized in California, apparently introduced from the Iberian Peninsula. Although the genus *Crupina* comprises two species in Spain, only one is known in the Western Hemisphere. This study compiled distribution maps for both *C. vulgaris* and *C. crupinastrum* in the Iberian Peninsula using 939 collections from 17 herbaria in Spain and 154 locations recorded in the literature (floras, botanical explorations, and phytosociological studies). *Crupina vulgaris* is more common, with a distribution occupying most of the eastern half of the Peninsula, reaching north to the southern slopes of the Pyrenees Mountains which form the boundary between Spain and France. It is rare in the western third of the Peninsula, including Portugal, and is absent on the Balearic Islands. Found throughout the southeastern quadrant of the Peninsula and Mallorca in the Balearic Islands, *Crupina crupinastrum* is most abundant in the Andalusian provinces. In southeastern Spain where their distributions overlap, *C. crupinastrum* is more prevalent than *C. vulgaris*. Detailed distribution maps in the native range of invasive species are useful for understanding biological invasions, comparisons of native and introduced habitats, and searches for potential biological control agents.

### RESUMEN

*Crupina vulgaris* es una planta de origen mediterráneo, de entre las 1045 especies naturalizadas en California, que se comporta como invasora y cuenta con poblaciones, relativamente recientes, en los condados de Sonoma y Modoc. Los estudios moleculares han demostrado que las cinco poblaciones norteamericanas derivan de 3 o más introducciones procedentes de la Península Ibérica. Aunque el género *Crupina* comprende dos especies en España, solamente una es conocida en el hemisferio occidental. En este estudio se presentan los mapas de distribución de *C. vulgaris* y *C. crupinastrum* en la Península Ibérica, obtenidas tras la revisión de 939 recolecciones encontradas en 17 herbarios de España y 154 referencias bibliográficas (floras, catálogos florísticos, y estudios fitosociológicos). *Crupina vulgaris* es la especie más común, con una distribución que ocupa la mitad oriental de la Península, alcanzando hacia el Norte las vertientes meridionales de los Pirineos. Es rara en el tercio oeste, incluyendo Portugal, y está ausente en las islas Baleares. Presente en todo el cuadrante suroriental de la Península y en Mallorca (islas Baleares), *Crupina crupinastrum* es más abundante en las provincias andaluzas. En el Sureste de España, donde ambas distribuciones se solapan, *C. crupinastrum* prevalece sobre *C. vulgaris*. Los mapas de distribución detallados de las especies invasoras en su zona de origen, son útiles para comprender las invasiones, la comparación entre hábitat autóctonos y alóctonos, y las investigaciones para buscar potenciales agentes de control biológico.

Key words: *Crupina crupinastrum*, *Crupina vulgaris*, invasive species, weed distribution

Among the 1045 alien plant species naturalized (17.5% of the flora) in California (Randall et al. 1998), *Crupina vulgaris* Cass. (Asteraceae: Cynareae) is a relatively recent addition. Rejmánek and Randall (1994) indicated that it was very likely introduced to California within the past 25 years. This contrasts sharply with numerous other Mediterranean species introduced in the Spanish and Mexican periods (1769–1848) (Bossard et al. 2000). When *Crupina vulgaris* was discovered in Idaho in 1968, it was reported in Madroño as a species new

to North America (Stickney 1972). Under the Federal Noxious Weed Act of 1974 (Public Law 93 629), *Crupina vulgaris* was included on the Federal Noxious Weed List as a new invader. Both *Crupina vulgaris* and its congener *Crupina crupinastrum* (Moris) Vis. were among 1200 species designated as economically important foreign weeds posing potential problems in the United States (Reed 1977). A search of the interception records for Federal Noxious Weeds by USDA APHIS PPQ from 1983 through 1998 showed that *Crupina vulgaris* has not been intercepted crossing the U.S. borders since it was listed and records kept on weed inter-

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ventions (Polly Lehtonen, USDA APHIS, personal communication).

Although the first flora in California to include *Crupina vulgaris* was The Jepson Manual (Hickman 1993), it was first discovered in California in 1976 at Santa Rosa, Sonoma County (unpublished CDFA reports, Miller and Thill 1983). It was subsequently discovered in 1984 at Lake Chelan, Chelan County, Washington (Alverson and Arnett 1986), and in 1987 at Dry Creek, Umatilla County, Oregon (Couderc-LeVaillant and Roché 1993). The Sonoma County population was declared eradicated by 1982 (Miller and Thill 1983), but it was rediscovered in 1989 about 1 km distant from the original infestation (unpublished CDFA records, Davis and Sherman 1991). In 1990 another new population was reported near Adin, Modoc County, California (unpublished CDFA records, Couderc-LeVaillant and Roché 1993). Thus, five infestations in four western States were detected between 1968 and 1990. *Crupina vulgaris* is inconspicuous due to its small, delicate stature and extremely difficult to detect when populations are sparse. All six original discoveries of *C. vulgaris* in the western United States were made by professional botanists or weed scientists; none were reported by casual observers or landowners.

Multiple introductions have been suspected for the invasion (Couderc-LeVaillant and Roché 1993; Patterson and Mortensen 1985), although a large propagule hinders long distance dispersal (Roché and Thill 2001). Since the previous publications in Madroño, earlier collections of *C. vulgaris* in North America have been reported from Massachusetts (Sorrie and Somers 1999). Specimens at the Harvard University Herbaria collected by C.E. Perkins in 1877 and 1879 from Boston and South Boston Flats, Suffolk County, Massachusetts (NEBC, W. Kittridge personal communication), indicate that *C. vulgaris* was among the numerous species introduced in ship's ballast from seaports in the Mediterranean region. Based on its absence in current floras, *C. vulgaris* failed to establish in the northeastern United States, and apparently arrived independently in western North America. Recent molecular studies (RAPD) revealed that the five current populations derived from three or more introductions from the Iberian Peninsula (Garnatje et al. 2002). Although the genus *Crupina* is represented by two species in the Iberian Peninsula and Balearic Islands, *C. crupinastrum* and *C. vulgaris*, only one has been reported in North America.

The objective of the study was to compile an accurate distribution map for *Crupina* in the part of its native range where its North American population founders originated. Such a map would serve as a foundation for further investigations, such as ecological studies comparing native and introduced habitats, including behavior of the invader, and factors that contribute to differences in species response in the two hemispheres. A distribution map

is also useful for searches for potential biological control agents. Floras provide general distribution information that is inadequate for these purposes. For example, Flora Europaea indicates that *C. vulgaris* grows on "dry grassland and stony slopes" in 17 countries (Amaral Franco 1976), which leads one to believe that it can be easily encountered anywhere in these habitats in southern Europe, as far north as west central France and the southern Ukraine. In fact, much of this distribution is based on centuries-old collection records, some of which represent localized populations that failed to persist under changing land use patterns in the past 100 years. In our study we included the more ruderal (within the Mediterranean region) congener, *C. crupinastrum*, in order to provide supporting information for inferences about plant migration and the invasion process.

#### METHODS

A complete listing of all recorded locations for both species of *Crupina* in the Iberian Peninsula was compiled from two types of sources: 1) literature citations of locations from floras, botanical explorations, and phytosociological studies and 2) herbarium specimens from 17 herbaria in Spain (listed in the acknowledgments, with institutional abbreviations from Holmgren et al. 1990). Because the two species closely resemble each other, each herbarium sheet was examined and annotated. On mature specimens, verification was based on cypselar characters, while immature specimens and others without fruits were verified using trichome characters (Couderc-LeVaillant 1984). Maps were prepared using software (CYANUS) based on 10 km UTM grid square.

#### RESULTS

The distributions of *C. vulgaris* and *C. crupinastrum* are shown on maps in Figs. 1 and 2, respectively. Of the 939 herbarium specimens examined, 572 were assigned to *C. vulgaris* and 367 to *C. crupinastrum*. The maps include 134 citations from the literature for which there was no doubt about the identification. An additional 120 literature citations for *C. vulgaris* were not included on the maps because they lacked corroborating herbarium vouchers and were from regions where the distribution of *C. crupinastrum* overlapped with that of *C. vulgaris*. In some provinces there were locality descriptions for which UTM coordinates could not be determined. A complete record of herbarium label and literature citations will be published in Spain (Gamarra and Roché 2002).

#### *Crupina vulgaris*

In the Iberian Peninsula, *C. vulgaris* is the more common species, with a distribution occupying most of the eastern half of the Peninsula (Fig. 1). All of the phytosociology literature and plant dis-

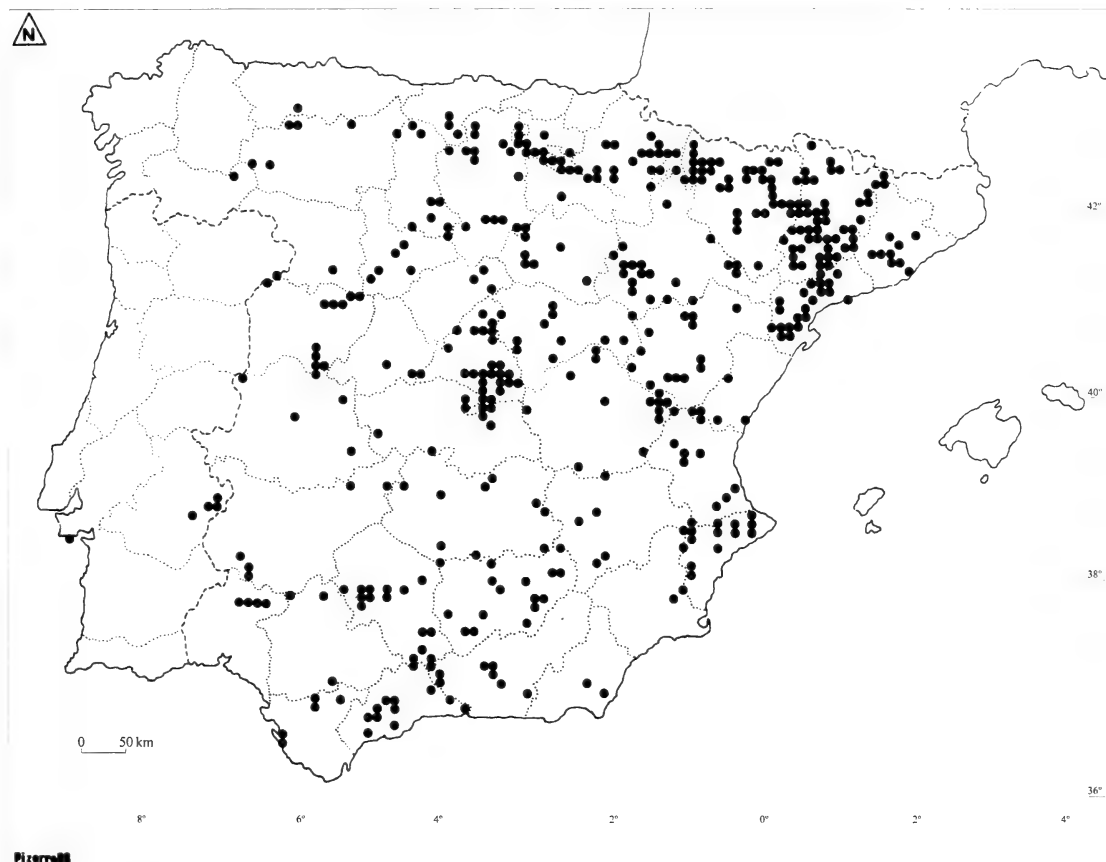


FIG. 1. Distribution of *Crupina vulgaris* in the Iberian Peninsula, each symbol indicates documented presence within a 10 km UTM grid square. Dotted lines are provincial boundaries; refer to Fig. 2 for names.

tribution records indicate that *C. vulgaris* is not found in forested areas and in subalpine grasslands, as well as areas of siliceous soils, which tend to be coarse and acidic. It does not occur on the Balearic Islands. The most northerly populations of *C. vulgaris* reach the southern slopes of the Pyrenees and the Pre-Pyrenean Mountains. In the western third of the peninsula its presence is sparser and almost always tied to calcareous substrates, which are infrequent in this region. In Portugal it is very rare, limited to certain populations near the locality of Elvas, very close to the border with Spain, and farther away, in Sezimbra, but always on calcareous soils. Using locations from herbarium labels dating from the 1970's, one of the authors (Roché) and a colleague searched all suitable habitat in the Elvas locality in 1999 and failed to find a single plant. If *C. vulgaris* is still present there, it is extremely scarce.

According to Rivas Martínez et al. (1990), this species appears in all the chorologic provinces, although in the north and northeastern provinces of Cántabro-Atlántica and Gaditano-Onubo-Algarviense, it occurs only in isolated locations. As stat-

ed earlier, in the history of Spanish botanical science, it has never been found in the Balearic province.

The elevation within its distribution ranges between 100 and 1200 (rarely 1500) m, reaching the major territory of the Sierra de Segura and the Pyrenees, but it is never found in the high mountains. It prefers basic soils, principally calcareous soils derived from limestone or clay soils rich in bases originating from evaporites (formed by the evaporation of brackish water), including substrates rich in gypsum; and is only rarely found over schist or slate. It is reported from rangeland, dry grazed areas, low matorral (e.g., thyme fields), open evergreen oak woodlands, and clearings in deciduous oak forests. It is also found along roadsides and on the margins of perennial crops such as vineyards or olive groves where they border appropriate native habitat.

#### *Crupina crupinastrum*

This species primarily inhabits the southeastern quadrant of the peninsula and the Balearic Islands,

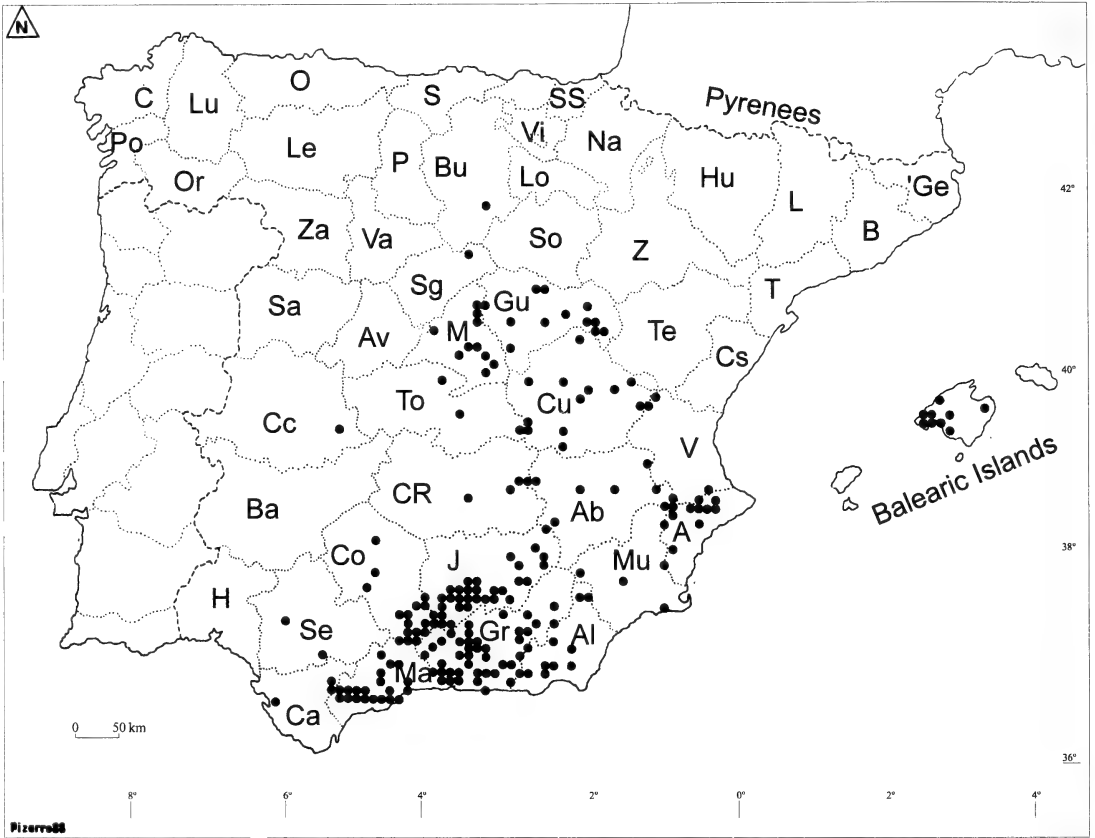


FIG. 2. Distribution of *Crupina crupinastrum* in the Iberian Peninsula, each symbol indicates documented presence within a 10 km UTM grid square. Abbreviations for names of provinces: Alicante (A), Albacete (Ab), Almería (Al), Asturias (O), Ávila (Av), Badajoz (Ba), Barcelona (B), Burgos (Bu), Cáceres (Cc), Cádiz (Ca), Cantabria (S), Castellón (Cs), Córdoba (Co), Ciudad Real (CR), Cuenca (Cu), Gerona (Ge), Granada (Gr), Guadalajara (Gu), Huelva (H), Huesca (Hu), Jaén (J), La Coruña (C), La Rioja (Lo), León (Le), Lugo (Lu), Madrid (M), Málaga (Ma), Murcia (Mu), Navarre (Na), Orense (Or), Palencia (P), Pontevedra (Po), Salamanca (Sa), Sevilla (Se), Segovia (Sg), Soria (So), Tarragona (T), Teruel (Te), Toledo (To), Valencia (V), Valladolid (Va), Vizcaya (Vi), Guipúzcoa (SS), Zamora (Za), Zaragoza (Z).

and is most abundant in the Andalusian provinces (Almería, Cádiz, Córdoba, Granada, Huelva, Jaén, Málaga, Sevilla) (Fig. 2). In contrast to the northern presence of *C. vulgaris*, *C. crupinastrum* only extends as far north as the provinces of Segovia and Burgos, where it is rarely encountered and could be interpreted as isolated individuals occurring as ephemeral introductions. In the Balearic Islands, it is found only on Mallorca. It does not appear on the Pitiusas Islands (the southwest islands within the Balearic group), which would be an extension of the levantian populations. Toward western Iberia, it is very rare and we found only isolated occurrences in the provinces of Sevilla (Castilleja de Guzmán) and Cáceres (Guadalupe), which did not extend as far as Portugal.

According to Rivas Martínez et al. (1990), this species appears principally in the provinces Bética and Castellano-Maestrazgo-Manchega, with some

presence in the provinces Murciano-Almeriense and Balear, and is very rare in the Luso-Extremadurens (Portugal, Cáceres and Badajoz).

The presence of *Crupina crupinastrum* is linked to basic soils, principally substrates of limestone and evaporites, although some populations in the province of Córdoba grow over schists. The elevation ranges between 100 and 1500 m, very rarely exceeding this limit, but occasionally doing so in the more southern mountains as in Gádor and in the Sierra Nevada. It appears on the sides of roads, grazed lands, pastures, low matorral, and open evergreen oak woodlands.

#### DISCUSSION

Both species of *Crupina* share the southeastern quadrant of the Iberian Peninsula, in some cases growing in mixed communities. In this region *C.*

*crupinastrum* is much more abundant than *C. vulgaris*. However, nowhere in the Iberian Peninsula would one describe either species as abundant in the plant communities where they occur. It is noteworthy that the more ruderal *C. crupinastrum*, which appears more frequently in disturbed sites (e.g., roadsides) than *C. vulgaris*, was not the species introduced in North America. Because cypselas of the two species are the same size with the same pappus characteristics, differing only in shape at the point of attachment (see illustrations in Reed 1977), this anomaly suggests that the invasion founders originated from locations where *C. crupinastrum* does not grow along with *C. vulgaris*.

On sites supporting *Crupina* in the Iberian Peninsula, grazing of sheep and goats is the primary land use, especially historically. In the Mediterranean region, *Crupina* has been identified among low chaparral species which maintain populations by epizootic transport associated with herds of domestic sheep and goats (Schmida and Ellner 1983). Transhumanant herds of sheep were likely the migratory vectors responsible for dispersing and maintaining isolated ephemeral populations in the Iberian Peninsula. Well established trails (cañadas) connect summer and winter pastures (Montserrat and Fillat 1990), which may be as close as mountain grasslands with adjacent valleys, or extend nearly the entire north-south distance of Spain (Mangas 1992).

The distribution of *C. vulgaris* far to the north of *C. crupinastrum* in the Iberian Peninsula is especially significant because the Pyrenean and Pre-Pyrenean Mountain region was the source of major immigration to the United States of laborers for the sheep industry through the early 1970's. Basque sheepherders were legendary in the western U.S. For example, in 1970 about 90% of the 1700 men under contract to the Western Range Association were Basques (Lane and Douglass 1985). Although the Spanish government required equal immigration opportunities for all Spanish nationals, it was primarily due to improving economic conditions in the Basque Country in the 1960's and 1970's that the numbers of Asturians, Leonese, Castellians and Andalusians swelled the herder ranks (Lane and Douglass 1985). After that time, this link with rural Spain ended when the range association shifted its herder recruitment efforts to Latin America and Mongolia.

Despite the recent (1968–1990) discoveries of *C. vulgaris* in western North America, it is probable that it arrived decades earlier. Arriving in small numbers to remote areas, with slow growing colonies of inconspicuous individuals, it is not surprising that it could escape detection for long periods of time. By showing where the distributions of *C. vulgaris* and *C. crupinastrum* overlap and diverge, and where the distribution of *C. vulgaris* overlaps a region that was home to numerous immigrants to rangelands of the western United States, these dis-

tribution maps provide a resource for elucidating the case history of how *C. vulgaris* became an invader in the Western Hemisphere, a chronicle that has not yet been fully revealed. They also serve as a reference for future studies concerning ecology and potential control.

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## HYMENOCLEAS ARE AMBROSIAS (COMPOSITAE)

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### ABSTRACT

Inclusion of *Hymenoclea* within the taxonomic circumscription of *Ambrosia* necessitates new combinations: *Ambrosia monogyra*, *A. ×platyspina*, *A. salsola*, *A. salsola* var. *fasciculata*, and *A. salsola* var. *pentalepis*.

Key words: *Ambrosia*, Compositae, *Hymenoclea*

After review of similarities and differences between and among species of *Hymenoclea* Torrey & A. Gray ex A. Gray and *Ambrosia* Linnaeus, especially with regard to restriction sites in chloroplast DNAs, Miao et al. (1995) concluded that the two species of *Hymenoclea* do not constitute a clade, are separately allied to franserioid members of *Ambrosia*, and are better included in *Ambrosia* than maintained as a distinct genus. They listed *Hymenoclea* as a synonym of *Ambrosia* Linnaeus subg. *Franseria* (Cav.) Miao et al., Pl. Syst. Evol. 194:252, 1995.

Baldwin et al. (1996) documented natural hybridization between *Hymenoclea salsola* Torrey & A. Gray ex A. Gray and the franserioid species *Ambrosia dumosa* (A. Gray) W. W. Payne and between *H. salsola* and *A. ambrosioides* (Cavanilles) W. W. Payne, another franserioid species. They noted "... normal pairing of chromosomes in interspecific hybrids" (i.e., between species of *Ambrosia* and *Hymenoclea*) as indicating "Close genetic similarity ..." of parental species and went on to say, "Hybridization between species of *Ambrosia* and *Hymenoclea* may reflect inadequacy of the long-standing generic classification of Ambrosiinae ..."

We have considered the findings of Miao et al. (1995) and Baldwin et al. (1996) and we are convinced that hymenocleas should be treated within the taxonomic circumscription of *Ambrosia*:

***Ambrosia monogyra*** (Torrey & A. Gray ex A. Gray) Strother & B. G. Baldwin, comb. nov. Basionym: *Hymenoclea monogyra* Torrey & A. Gray ex A. Gray, Mem. Amer. Acad. Arts n.s. 4: 79. 1849. Syntypes: "Along the valley of the Gila, Lieut. Emory. Also at 'Ojito,' New Mexico? Dr. Gregg." Peterson and Payne (1973, p. 253–254) cited the Emory collection at NY as type and thereby effected lectotypification.

***Ambrosia salsola*** (Torrey & A. Gray ex A. Gray)

Strother & B. G. Baldwin, comb. nov. Basionym: *Hymenoclea salsola* Torrey & A. Gray ex A. Gray, Mem. Amer. Acad. Arts n.s. 4:79. 1849. Type: California, "Sandy, saline uplands near the Mojave River, . . . , Fremont." Lectotype (Peterson and Payne 1973, p. 254): 1844, *Fremont 400* (NY).

***Ambrosia salsola*** (Torrey & A. Gray ex A. Gray) Strother & B. G. Baldwin var. ***fasciculata*** (A. Nelson) Strother & B. G. Baldwin, comb. nov. Basionym: *Hymenoclea fasciculata* A. Nelson var. *fasciculata*. [cf. *Hymenoclea fasciculata* A. Nelson, Bot. Gaz. 37:270. 1904. Type: Nevada, "Kernan," 29 Apr 1902, *L. N. Goodding 662* (NY). The variety *fasciculata* dates from publication of *Hymenoclea fasciculata* A. Nelson var. *patula* A. Nelson, Bot. Gaz. 47:431. 1909. Type: Nevada, "Moapa," 8 Apr 1905, *L. N. Goodding 2178* (RM). Peterson and Payne (1973, 1974) treated the two types, *Goodding 662* and *2178*, as convarietal. Initially, Peterson and Payne named that variety *Hymenoclea salsola* Torrey & A. Gray ex A. Gray var. *fasciculata* (A. Nelson) K. M. Peterson & W. W. Payne (Brittonia 25:255. 1973). Under the applicable Code (Stafleu et al. 1972) in 1973, Peterson and Payne should have used the varietal epithet "*patula*" because autonyms were "not to be taken into consideration for purposes of priority." Peterson and Payne subsequently renamed that same variety *Hymenoclea salsola* Torrey & A. Gray ex A. Gray var. *patula* (A. Nelson) K. M. Peterson & W. W. Payne (Brittonia 26:397. 1974), which is now an illegitimate name because under the current Code (Greuter et al. 2000), the autonymic varietal name has priority at varietal rank.]

***Ambrosia salsola*** (Torrey & A. Gray ex A. Gray) Strother & B. G. Baldwin var. ***pentalepis*** (Rydberg) Strother & B. G. Baldwin, comb. nov. Basionym: *Hymenoclea pentalepis* Rydberg in N. L.

Britton et al., N. Amer. Fl. 33:14. 1922. Type: Arizona, "Pima Cañon," 10 Apr 1901, *D. Griffiths* 2630 (NY)  $\equiv$  *Hymenoclea salsola* Torrey & A. Gray ex A. Gray var. *pentalepis* (Rydberg) L. D. Benson, Amer. J. Bot. 30:631. 1943.

*Hymenoclea hemidioica* A. Nelson, Amer. J. Bot. 25:117. 1938. Syntypes: Arizona, Mohawk Mountains, 29 Mar 1935, A. Nelson 1340 and 1341 (RM?, not seen).

We use the name ***Ambrosia*  $\times$  *platyspina*** (Seaman) Strother & B. G. Baldwin, comb. nov. [Basionym: *Hymenoclea*  $\times$  *platyspina* Seaman, Madroño 23:111. 1975, pro sp.], for hybrids between *A. dumosa* and *A. salsola*.

We believe the name *Ambrosia sandersonii* S. L. Welsh, Rhodora 95:396. 1993[1994] [ $\equiv$  *Hymenoclea sandersonii* (S. L. Welsh) N. H. Holmgren in A. Cronquist et al., Intermount. Fl. 5:473. 1994], also refers to hybrids, perhaps to hybrids between *A. eriocentra* (A. Gray) W. W. Payne and *A. salsola* (Baldwin et al. 1996). We treat Welsh's name as *Ambrosia*  $\times$  *sandersonii* S. L. Welsh, pro sp.

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## THE FLORA OF TORO ISLET AND NOTES ON GUADALUPE ISLAND, BAJA CALIFORNIA, MEXICO

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### ABSTRACT

During a natural history expedition to Guadalupe Island and its adjacent islets in June of 2000, the previously unexplored islet, Toro, was botanically surveyed. The flora of this islet was found to have 32 species and one putative interspecific hybrid. This diversity represents 30 dicots and 2 monocots, in 22 plant families. Eighteen of the plant taxa are endemic to the Guadalupe Island group, resulting in a 56.3% endemism in the islet's flora. A few native plant communities were observed on the islet, within which only three plant taxa are obviously exotic, rare in occurrence, and presumably introduced by seabirds. The botanical data obtained from this undisturbed islet helps us to fill in the missing pieces about the overall flora of Guadalupe Island and its adjacent islets especially in relation to the ecological devastation caused by feral goats on the main island. Brief notes on other floristic components of Guadalupe Island and its islets, and new plant records collected during the expedition are also presented.

### RESUMEN

Durante una expedición para estudiar la historia natural de la Isla Guadalupe e islotes adyacentes, en junio de 2000, inventariamos la flora del islote Toro, que nunca había sido explorado. En este islote encontramos 32 especies de plantas y un aparente híbrido interespecífico, incluyendo 30 dicotiledonas y 2 monocotiledonas, de 22 familias. Dieciocho de los taxa son endémicos a la Isla Guadalupe e islotes adyacentes, por lo tanto Toro tiene una tasa de endemismo de 56.3%. Se encontraron algunas comunidades de plantas nativas, en las que solamente 3 taxa eran exóticas, poco abundantes, probablemente introducidas por aves marinas. La información botánica de este islote sin disturbio puede ayudarnos a llenar las piezas faltantes de la flora de Guadalupe, especialmente en relación con la devastación ecológica causada por cabras en la isla principal. Además, en este artículo presentamos notas breves sobre otros componentes florísticos de la Isla Guadalupe y sus islotes, y nuevos registros de plantas colectadas durante la expedición.

Key words: Guadalupe Island, Baja California, Mexican flora, expedition, endemism

The Guadalupe Island Expedition in June of 2000 involved 16 scientists from the U.S.A. and Mexico representing arachnology, botany, conservation biology, entomology, marine ecology, ornithology, and phycology. This expedition was organized by the San Diego Natural History Museum and funded by the Biotic Surveys and Inventories section of the National Science Foundation (Grant No. 0074462). The primary emphases of this binational, multidisciplinary endeavor were to observe, record, and collect natural history information on the biodiversity of Guadalupe Island and the previously unexplored Toro Islet. The botanists of the expedition were Dr. José Luis León de la Luz of the Centro de Investigaciones Biológicas del Noroeste, Tom Oberbauer of the Department of Planning and Land Use for the County of San Di-

ego, and Dr. Exequiel Ezcurra, and the senior author from the San Diego Natural History Museum.

The biological data obtained on this trip provides us with additional biodiversity information on all of the terrestrial areas of Guadalupe Island and its islets and will be used for making conservation decisions for the island and evaluating the impacts of introduced species such as feral goats and cats. The floristic information from the expedition can be used to supplement our current knowledge on the entire Guadalupe Island flora as presented by Moran (1996).

### THE ISLAND ENVIRONMENT

Guadalupe is an oceanic island located approximately 260 km off the Pacific coast of the Baja

California peninsula, in northwestern Mexico. The island's general geographic position is 29°03'N latitude and 118°17'W longitude. Guadalupe Island is about 36 km long on its N-S axis and 12 km wide on the E-W axis, with an approximate surface area of 250 km<sup>2</sup>. The island is the peak of a seamount, which may have originated from several eruptive episodes, with the oldest exposed rocks being dated around 7 million years old (Moran 1996). There are three islets off of the southern end of the main island: Negro (30 m in elevation), Toro (220 m), and Zapato (190 m). Each islet has approximately 1 km<sup>2</sup> of surface area.

The climate of the island is maritime and heavily influenced by the cold California Current, with its characteristic features of wind, fog, and winter rainfall. A meteorological station on the southern end of Guadalupe (the driest area of the island) indicates almost 120 mm of rainfall annually and a mean monthly temperature of 17–19°C that is relatively stable throughout the year. It should be noted that the annual precipitation value given above does not include the contribution of moisture from fog condensation, which is a common event on Guadalupe Island.

Floristically, the island is considered an "outlier" of the California Floristic Province (Moran 1996) since it is composed of many native plant species either disjunct from this vegetation type on the mainland or on other islands, or endemic species with northern affinities. Although the island is home to Mexico's only populations of many plant species from the California Floristic Province, its most striking attribute is its endemism, which occurs in many biological groups. According to Moran (1996) in respect to plants, almost 22% of the native species are endemic, including two monospecific genera. Although there have been 220 different plant taxa documented over time on Guadalupe Island and its islets, the activities of feral goats released in the early 19th century by whalers have devastated most of the main island's flora. This impact on the flora is not only from the direct browse of goats, but also from the damage to the insular substrates as a result of soil erosion. At present, the main island's original flora and natural plant communities have practically vanished. It is estimated (Moran 1996) that at least 26 native plant species could now be extinct, including one endemic, monospecific genus and many other plant species seem to be on the threshold. To add to the problem, the vegetation is now dominated mainly by weedy species; 62 exotic plant taxa have been recorded on the island, of which many are quite aggressive and capable of competing for niches and displacing native species.

Toro (also known as Islote de Adentro or Inner Islet) is a small islet that lies directly off of the southern end of Guadalupe Island, situated between the main island and another southern islet, Zapato. Toro Islet is a dome-shaped rock that reaches ap-

proximately 500–700 feet (165–220 m) in elevation. The islet has very steep, vertical walls that arise out of the water at an angle of almost 90 degrees and that have, heretofore, prohibited its exploration. However, during this expedition the scientists used a helicopter to facilitate landing and exploration on the islet. On its top, Toro has a small basin in its center with a high western ridge. A narrow ridge extends to the north and drops into a steep slope facing the main island. There are two types of rocky substrates that exist on this volcanic islet. One type of substrate is a rocky, fractured basaltic material with darker coloration and the other is a tan, hard solid rock with characteristics of andesite. Plant species occur on both substrates but most seem to prefer the broken basaltic materials.

#### THE FLORA OF TORO

The known flora (see Table 1) of Toro Islet that was documented during the expedition consists of 32 species and 1 putative hybrid. This diversity represents 30 dicots and 2 monocots, in 22 plant families. Eighteen of the taxa are endemic to Guadalupe Island, resulting in a 56.3% rate of endemism in the islet's flora. The Asteraceae are the best represented on the islet with 5 genera, 6 species and one putative interspecific hybrid in the genus *Hemizonia*. Other families such as Malvaceae, Scrophulariaceae, and Fabaceae are represented with two genera. Only *Cryptantha*, *Hemizonia*, and *Mesembryanthemum* are represented with two species in the same genus.

Only three plant taxa (*Hordeum murinum* ssp. *glaucum*, *Mesembryanthemum crystallinum*, and *M. nodiflorum*) are obviously exotic. As of yet, their populations on the islet are small and their occurrences quite rare. It is likely that they are rather recent introductions, which presumably arrived by seabirds. In fact, *Hordeum* seems to be currently confined to the steep northern slope of the islet in an area near Western Gull (*Larus occidentalis*) nests.

Of the 32 plant species found on the islet, eleven are succulent in nature with fleshy leaves, stems, or both, and are represented by species in eight different plant families (Rebman 2001). Six of these succulent taxa are endemic to the Guadalupe Island and its adjacent islets. One of the leaf succulent species, *Baeriopsis guadalupensis* belongs to an endemic, monotypic genus in the Sunflower family (Asteraceae).

The vegetation of Toro Islet is best described as a maritime, succulent scrub and is similar to that found on the other southern islets, Zapato and Negro. This type of vegetation probably dominated most of the southern portions of the main island as well, but is mostly extirpated now by the impacts of feral goats. This vegetation is dominated by *Atriplex barclayana*, *Cistanthe guadalupensis*, *Euphorbia misera*, *Spergularia macrotheca* var. *talinum*,

TABLE 1. FLORISTIC LIST OF TORO ISLET, BAJA CALIFORNIA, MEXICO. Note that Coll. # refers to the collection numbers of plant specimens made by Rebman et al.

Plant taxon (family)	Coll. #
<i>Atriplex barclayana</i> (Benth.) D. Dietr. (Chenopodiaceae)	6753, 6763
<i>Baeriopsis guadalupensis</i> J. T. Howell (Asteraceae)	6758, 6882
<i>Castilleja fruticosa</i> Moran (Scrophulariaceae)	6774
<i>Cistanthe guadalupensis</i> (Dudley) Carolin in Hershkovitz (Portulacaceae)	6765
<i>Coreopsis gigantea</i> (Kellogg) H. M. Hall (Asteraceae)	6759
<i>Cryptantha foliosa</i> (Greene) Greene (Boraginaceae)	6781a
<i>Cryptantha maritima</i> (Greene) Greene var. <i>maritima</i> (Boraginaceae)	6781b
<i>Dichelostemma capitatum</i> Alph. Wood ssp. <i>capitatum</i> (Themidaceae)	6773
<i>Dudleya guadalupensis</i> Moran (Crassulaceae)	6757
<i>Erysimum moranii</i> Rollins (Brassicaceae)	6772
<i>Eschscholzia palmeri</i> Rose (Papaveraceae)	6755
<i>Euphorbia misera</i> Benth. (Euphorbiaceae)	6779
<i>Galvezia speciosa</i> (Nutt.) A. Gray (Scrophulariaceae)	6761
<i>Hemizonia greeneana</i> Rose ssp. <i>greeneana</i> (Asteraceae)	6756, 6766
<i>Hemizonia hybrid</i> (Asteraceae)	6775
<i>Hemizonia palmeri</i> Rose (Asteraceae)	6760
<i>Hordeum murinum</i> L. ssp. <i>glaucom</i> (Steud.) Tzvelev. (Poaceae)	6770
<i>Lavatera lindsayi</i> Moran (Malvaceae)	6754, 6764
<i>Lomatium insulare</i> (Eastw.) Munz (Apiaceae)	6780
<i>Lotus argophyllus</i> (A. Gray) Greene ssp. <i>ornithopus</i> (Greene) Raven (Fabaceae)	6769
<i>Lupinus niveus</i> S. Watson (Fabaceae)	6778
<i>Lycium californicum</i> Nutt. (Solanaceae)	6884
<i>Mammillaria blossfeldiana</i> Boed. var. <i>shurliana</i> (Gates) Wiggins (Cactaceae)	6784
<i>Mesembryanthemum crystallinum</i> L. (Aizoaceae)	6767
<i>Mesembryanthemum nodiflorum</i> L. (Aizoaceae)	n/a
<i>Mirabilis laevis</i> (Benth.) Curran var. <i>crassifolia</i> (Choisy) Spellb. (Nyctaginaceae)	6777
<i>Perityle incana</i> A. Gray (Asteraceae)	6776
<i>Phacelia floribunda</i> Greene (Hydrophyllaceae)	6782
<i>Plantago ovata</i> Forssk. (Plantaginaceae)	6783
<i>Rhus integrifolia</i> (Nutt.) Brewer & S. Watson (Anacardiaceae)	6771
<i>Spergularia macrotheca</i> (Hornem.) Heynh. var. <i>talinum</i> (Greene) Jepson	6762
<i>Sphaeralcea palmeri</i> Rose (Malvaceae)	6768
<i>Stephanomeria guadalupensis</i> Brandege (Asteraceae)	6883

*Sphaeralcea palmeri*, and *Stephanomeria guadalupensis*. The succulent, perennial *Cistanthe guadalupensis* appears to be the most common of all of the species on the islet. It was in full flower during our visit in the early part of June, but other conspicuously flowering species included *Baeriopsis guadalupensis*, *Eschscholzia palmeri*, *Perityle incana*, and two species of *Hemizonia*. The plant community of the central basin on the islet is dominated by *Atriplex barclayana*, *Cistanthe guadalupensis*, and *Sphaeralcea palmeri* with a strong presence of *Dudleya guadalupensis*, *Euphorbia misera*, *Lavatera lindsayi*, *Lycium californicum*, *Mammillaria blossfeldiana* var. *shurliana*, *Spergularia macrotheca*, and *Stephanomeria guadalupensis*. On the upper slopes of the basin *Baeriopsis guadalupensis*, *Coreopsis gigantea*, *Eschscholzia palmeri*, *Hemizonia greeneana* ssp. *greeneana*, and *H. palmeri* are prominent. The endemic *Stephanomeria guadalupensis* is most common on the lower slopes and bottom of the basin. The steep northern slope was the only location where *Erysimum moranii*, *Phacelia floribunda* and *Rhus integrifolia* were found. One individual plant of a putative interspecific hybrid between *Hemizonia greeneana* ssp.

*greeneana* and *H. palmeri* was found on the northern ridge.

The flora of Toro Islet is very similar to that of Zapato Islet (also known as Islote de Afuera or Outer Islet) with a few exceptions. It is noteworthy that *Eriogonum zapatoense* was not found on Toro, though an effort was made to look for it. This endemic buckwheat species apparently only occurs on Zapato, where it is found on the upper ridge and basin rim and is relatively common there. Similar habitats were examined on Toro Islet, but it was not seen. Zapato Islet has a large basin that drops down to near sea level where plants such as *Aphanisma blitoides* occur. In general, Zapato appears to have a greater diversity of habitat types than Toro. Other species that occur on Zapato and not on Toro are *Atriplex californica*, *Calystegia macrostegia* ssp. *macrostegia*, *Crassula connata*, *Crossosoma californica* (which may no longer occur on Zapato), *Descurainia pinnata* ssp. *menziesii*, *Hutchinsia procumbens*, *Lavatera occidentalis*, *Oligomeris linifolia*, *Parietaria hespera* var. *hespera*, *Perityle emoryi*, and *Pholistoma racemosum*. Plant taxa found on Toro Islet and not on Zapato include: *Cryptantha maritima*, *Hemizonia palmeri*, a puta-

tive *Hemizonia* hybrid, *Hordeum murinum*, *Lupinus niveus*, *Mesembryanthemum nodiflorum*, and *Plantago ovata*. All of these plants are found on the adjacent main island, which lies in closer proximity to Toro.

While Toro Islet was explored quite fully, there are still possibilities for plants that were missed, particularly annual species. A botanical survey of Toro in early spring of a rainy year would probably identify additional annuals in the islet's flora in genera such as *Descurainia*, *Hutchinsia*, *Oligomeris*, *Parietaria*, and *Pholistoma*, all of which have been recorded on Zapato Islet.

#### MISCELLANEOUS BOTANICAL NOTES AND OBSERVATIONS FROM THE EXPEDITION

In total, 149 plant collections were made during the entire expedition of which, four specimens document new distributional records for both native and exotic species not previously known to occur on the island. The new records of naturalized, exotic species include: *Atriplex rosea* L. (Rebman *et al.* 6817) and *A. semibaccata* R. Br. (Rebman 6750), both found near the airstrip in the center of the main island; and *Schismus barbatus* (L.) Thell. (Rebman 6752) found in the vicinity of the Northeast Anchorage along the trail in Barracks Canyon.

Of particular note was the discovery of a new native species for the island, *Lonicera hispidula* Douglas var. *vacillans* A. Gray. This pink-flowered honeysuckle is also found on Santa Cruz, Santa Catalina, and San Clemente islands of California, but is the first record (Rebman *et al.* 6800) of its occurrence in Mexico. Only one individual plant was found on the upper parts of a 5-meter-high rocky cliff cascade.

Moran (1996) lists the weedy exotic *Chamomilla suaveolens* (Pursh) Rydb. (= *Matricaria matricarioides* (Less.) Porter) as part of the Guadalupe flora, but it should be noted that the specimen (Wiggins & Ernst 113) upon which this is based was misidentified and is actually the native species *C. occidentalis* (E. Greene) Rydb. Another plant species, *Dichelostemma capitatum*, was listed in Moran (1996) as possibly introduced to Guadalupe Island. However, its presence on Toro and Zapato as well as on major portions of the main island does not support the concept that it was introduced.

In preparation for the expedition, all of the data from specimens previously collected on Guadalupe Island and its adjacent islets that are housed in the SD Herbarium were compiled into a database. Digitized images, mostly scanned herbarium specimens, of the endemic plant taxa for the island archipelago were also captured.

Botanical specimens collected on the expedition were done so in replicate, whenever possible, so that specimens would be available for study in several herbaria. The first collections will be deposited at the SD Herbarium of the San Diego Natural His-

tory Museum, and duplicates will be in Mexican herbaria at HCIB in La Paz and BCMEX in Ensenada. Plant materials including seeds and/or specimen samples for genetic analyses were collected and sent to several institutions. Samples of species in the Asteraceae including *Baeriopsis*, *Perityle incana*, *Stephanomeria*, and the putative *Hemizonia* hybrid material were sent to the Jepson Herbarium (UC/JEPS) at the University of California Berkeley. Leaf material of *Castilleja fruticosa* was sent to the University of Washington (WTU) and samples of *Lavatera lindsayi*, *Lupinus niveus*, and *Phacelia floribunda* were sent to the University of South Dakota. *Triteleia guadalupensis* material was sent to the University of Wisconsin for research on the Themidaceae.

While conducting botanical explorations on Zapato Islet during the expedition, some observations were made on the reproductive biology of two plant species endemic to the Guadalupe Island group. These observations are based only on morphology and their functionality still needs to be investigated further. It appears that *Mammillaria blossfeldiana* var. *shurliana* is a gynodioecious species with two sexual conditions. Although many of the cacti were not in flower at the time of our visit, a few flowering individuals showed evidence for two flower types occurring on different plants. Most flowering individuals appeared to have only bisexual flowers, with both functional stamens and pistils. However, a few plants were obviously different and seemed to be functionally female. These pistillate individuals had flowers with smaller tepals, abortive anthers not producing pollen, and pistils with a larger size and increased number of stigmatic lobes. Plants showing these different floral characteristics grew in the same immediate vicinity on the islet. Gynodioecy is not uncommon in the *Mammillaria* species of Baja California since it has been documented in *M. dioica* and some of its relatives in the region (Lindsay and Dawson 1952). However, this is the first report of this sexual condition in this cactus species.

The other notable flower forms occurred in *Cistanthe guadalupensis*. Some individuals had flowers with "normal-sized" petals (corolla diameter approximately 3–4 cm.) and yellow anthers, while other plants had "normal-sized" flowers but had pink-purple anthers. Furthermore, a fewer number of individual plants had significantly smaller flowers (corolla diameter approximately 2 cm.) and much shorter inflorescences. These plants with smaller flowers and inflorescences exhibited only yellow anthers and no fruit formation was seen. All of these three different flower forms were observed on individuals growing in close proximity to one another on Zapato. The comparable stages of flowering and similar moisture conditions of the local habitat seem to rule out any environmental cause for these floral variations. Therefore, it is hypothesized that *Cistanthe guadalupensis* is an andro-

dioecious species. It appears that the individuals that have smaller flowers, shorter inflorescences, and no fruit formation are functionally staminate, while the plants with "normal-sized" flowers and viable pistils that develop into fruits are hermaphrodites. The variability in anther color on different hermaphroditic plants is not yet understood and may not affect the reproductive system of this species.

#### CONCLUSION

The botanical data obtained from Toro Islet during this expedition not only helps to fill in the missing pieces about the overall flora of Guadalupe Island and its adjacent islets, but it also yields important information for conservation efforts. Due to the extinction of various plant species as a result of the ecological devastation caused by feral goats on the main island, the undisturbed Toro Islet is a very important resource for plant taxa that can be used for restoration of the main island if and when the goats are removed. The diversity of native and endemic plants in this region is a rich heritage and serious conservation strategies need to be implemented in order to lessen the threats for their survival into the future.

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GENETIC STRUCTURE OF *SENECIO LAYNEAE* (COMPOSITAL):  
A RARE PLANT OF THE CHAPARRAL

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ABSTRACT

The genetic structure of *Senecio layneae*, a rare plant endemic to the fire adapted chaparral in the central foothills of the Sierra Nevada, California, USA, was investigated over the entire known range of the species. Genetic variation was assessed using 63 ISSR and 42 RAPD polymorphic DNA markers. Multivariate analysis differentiated populations from each of three counties and grouped two populations from El Dorado County together. ISSR markers more accurately portrayed population membership patterns than did RAPD markers. A species-wide  $F_{ST}$  of 0.28 (by AMOVA) and a  $F_{ST}$  of 0.22 within El Dorado County showed that significant genetic differentiation exists in the species and between local (within 5.5 km) populations. These results argue for maintenance of disturbed openings in the chaparral which this federally listed, threatened species can recolonise after fire, and for the use of local seed sources (within 5.5 km) for re-introduction efforts. Additionally, the preservation of multiple populations is indicated in order to maintain the existing pattern of genetic diversity across the landscape.

Key words: ISSR, RAPD, genetic structure, *S. layneae*, chaparral

*Senecio layneae* E. L. Greene (Compositae), Layne's Butterweed, is a perennial herb with an underground rootstock that forms small clones. It is restricted to open rocky areas within chaparral plant communities on gabbroic or serpentine-derived soils in the central Sierran foothill counties of Yuba, El Dorado, and Tuolumne in California (California Native Plant Society 1994; USFWS 1996). Plants occur in sunny openings within the chaparral and die off as vegetation grows up around them (Baad and Hanna 1987). Flowering between April and June, the inflorescence is composed of disk flowers and a handful of unevenly distributed ray flowers. Primarily insect pollinated (G. Marsh personal observation), its dandelion-like seeds are suitable for dispersal by the wind. It is not known if a persistent, heat resistant seed bank of *S. layneae* exists in the soil beneath the chaparral.

*Senecio layneae* was federally listed as threatened in 1996 (USFWS 1996). Chief threats include residential and commercial development, road maintenance, decreased fire frequency, off-road vehicle use, competition from invasive alien vegetation, shading from native tree and shrub species, excessive horse grazing practices and gold mining (USFWS 1996). Populations of between 3 and perhaps 1000 plants (M. Baad personal communication) are scattered within the chaparral of western El Dorado County including the Pine Hill gabbroic

intrusion and adjacent serpentine (USFWS 1996). In Tuolumne County, several populations of between 2 and 500 plants (A. Franklin personal communication) were first documented in 1984, and occur in the chaparral dominated BLM Red Hills Management Area (BioSystems Analysis, Inc. 1984). In Yuba County two populations, one of approximately 200 plants on public land, and the other composed of scattered plants found on private lands, are found in chaparral and open Ponderosa Pine forest (Bureau of Land Management 1997). They were first reported in 1997, expanding the range of *S. layneae* northward 93 km.

The protection of genetic diversity within species has become a priority for conservation efforts (Holsinger and Gottlieb 1991; Falk 1992). Such genetic diversity may be evident between individuals within a population or between the populations in a region. The long-term objective is to maintain the evolutionary viability of the taxon, and maximize its chances for persistence in the face of changing environments (Huenneke 1991). Genetic diversity contributes to short-term ecological success in the face of stochastic environmental events such as local population destruction, pathogens, or herbivory (Holsinger and Gottlieb 1991). In rare plant preserve planning, an effort to preserve the species' entire genetic diversity must be a goal (Frankel and Soule 1981).

The genetic variation maintained within a species is distributed among regions, populations, and individuals within populations (Barrett and Kohn

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1991). Variation in rates of gene flow, intensity of natural selection, and random genetic drift create a hierarchy which is referred to as genetic structure. Genetic structure arises when gene flow between populations is limited, favoring development of distinct arrays of genetic characters within each population (Wright 1951; Nei 1973). It is important to determine the spatial scale at which differentiation of populations occurs in order to understand the pattern of population divergence and microevolution of a species. Preservation of this pattern should be a priority for species conservation (Driscoll 1998).

Several life history factors, primarily those related to pollen and seed dispersal, have been associated with the development of genetic structure (Hamrick and Godt 1989). Wind carried seed, and an outcrossed breeding system, such as occurs in *Senecio layneae* (G. Marsh personal observation), promote gene flow, hampering the development of genetic structure and reducing the affects of genetic drift. Alternatively, *Senecio layneae* appears to recolonize sunny openings left in the chaparral after disturbance such as fire or brush clearing, resulting in a historically patchy distribution. Small, patchily distributed populations would lead to the development of genetic structure through drift. Our primary research goal was to examine the genetic structure of this species and to infer the spatial scales at which gene flow is common and rare. Additionally, we will infer how historical fire regime could have influenced the genetic structure of populations seen today.

Previously, much information about the genetic structure of plants was based almost entirely on data from electrophoretic surveys of soluble enzymes (allozymes). Recently, RAPD-PCR-based methods have been used to investigate plant genetic structure (i.e., Huff et al. 1993; N'Goran et al. 1994; Baruffi et al. 1995; Ayres and Ryan 1997; Martin et al. 1997). These nuclear genetic markers are presumed to be selectively neutral and can reveal patterns in variation due to neutral process such as random genetic drift and gene flow. This knowledge does not necessarily inform us regarding the arrangement of adaptively important traits across the landscape (Olfelt et al. 2001). However, even with these limitations, information from molecular markers provides insight into population isolation due to restricted gene flow, and divergence due to drift which are potent factors in species evolution.

A new type of marker, ISSR (inter-simple sequence repeat), appears to be even more efficient than RAPD's (random amplified polymorphic DNA's) and has been used in recent investigations of natural plant populations (Robinson et al. 1997; Wolfe et al. 1998a, b; Esselman et al. 1999). ISSR markers are repeat-anchored primers that amplify regions between SSR's (simple sequence repeats or microsatellites) (Tsumura et al. 1996). ISSR primers an-

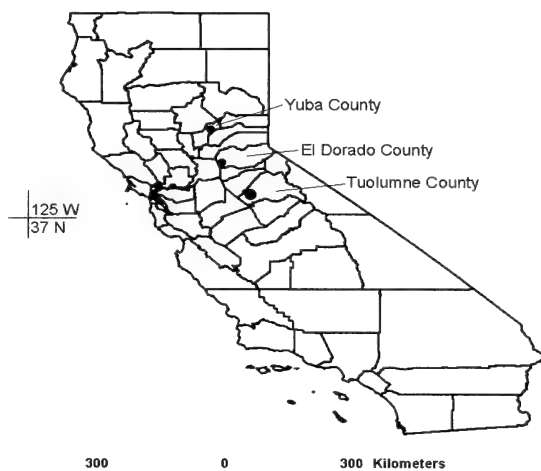


FIG. 1. Locations of four sample sites for *Senecio layneae* in Yuba County, El Dorado County, and Tuolumne County, California, 1999.

neal directly to SSR's and no prior knowledge of the genome is required (Tsumura et al. 1996; Wolfe and Liston 1998). Additionally, ISSR's produce a complexity of patterns as well as a level of polymorphisms detected per single PCR experiment that largely exceeds that of RAPD's (Zietkiewicz et al. 1994; Esselman et al. 1999; Ajibade et al. 2000). They are interpreted as dominant markers similar to RAPD data and are scored as binary data with 'band present' or 'band absent' (Wolfe et al. 1998a). Our secondary research goal was to compare the accuracy of ISSR and RAPD markers in determining genetic structure in *S. layneae*.

## MATERIALS AND METHODS

### Sample Collection

Plant material was collected in the early spring when the dormant rootstocks began producing new growth. Four sites were sampled: Yuba County near Brownsville, Pine Hill and Cameron Park in El Dorado County, and the Red Hills in Tuolumne County (Fig. 1). One apical meristem was removed from 20 individuals from each of four populations. Plants were patchily distributed and sampled individuals were haphazardly chosen at least 2 meters apart to avoid sampling the same individual twice. Each sample was placed on ice until returned to the lab at which time they were stored at  $-70^{\circ}\text{C}$  until DNA was extracted.

### DNA Extraction

DNA was extracted according to Ayres and Ryan (1997) with the addition of a RNAase treatment between the two alcohol precipitations: 100  $\mu\text{l}$  of TE (10 mM Tris-HCL and 1 mM EDTA, pH 7.8) and 1 unit of RNAase (Sigma) were added to the

first DNA pellet and the tubes were then incubated at 35°C for 20 min. Precipitation in ethanol followed. The DNA was quantified from the absorbance at 260 nm in a spectrophotometer.

### PCR and Electrophoresis

Prior to screening primers, the optimum PCR annealing temperature was determined by running a temperature gradient reaction using a single accession. The optimum annealing temperature was found to be 39°C for RAPD's, and 54°C for ISSR's. Amplification was performed with the following thermocycler programs: for RAPD's, 94°C for 15 sec, 39°C for 30 sec, 72°C for 2.0 min, repeated 40 times, and then a 4°C holding temperature; for ISSR's the program was identical except that the annealing temperature was 54°C.

RAPD and ISSR PCR were performed in an Eppendorf Mastercycler gradient (Westbury, NY). DNA amplification reactions were performed in a volume of 15 µl containing approximately 30 ng of plant DNA, 0.20 µM/liter primer (Operon Technologies, Inc., Alameda, CA, primers A4, C1, C8, C10, D7, G8, G13, G14, G18, G19, H9 for RAPD); University of British Columbia kit 800, primers 807, 823, 836, 846, 848, 857, 859, 860 for ISSR), 200 µM/liter each of dATP, cCTP, dGTP, dTTP (Promega, Madison, WI), 0.6 units Taq polymerase (Promega, Madison, WI), 3 µmol/liter MgCl<sub>2</sub>, 10% by volume MgCl<sub>2</sub>-free 10× reaction buffer A (Promega, Madison, WI), and 10.5 µl of double distilled water. The reaction mixture was overlain with a drop of mineral oil. PCR products were loaded on to 1.5% agarose gels for electrophoresis in 0.50× TBE buffer, followed by staining in ethidium bromide, and visualized and photographed under UV light. Molecular sizes of the visualized bands were estimated by referencing a 100 base-pair ladder (Gibco Co.). Polymorphic, reproducible bands were scored as present or absent.

Eighty-four decanucleotide RAPD primers from Operon Technologies, Inc. (Alameda, CA) and 84 ISSR primers from the University of British Columbia were screened against one DNA sample to find primers that amplified DNA of *S. layneae*. The primers that produced bands were then subjected to a second evaluation using one accession from three populations (Yuba, Cameron Park, Pine Hill). Primers that amplified DNA from all three populations were subjected to a third screening using three accessions from each of the three populations (9 total DNA samples) to identify primers that produced polymorphic bands. Each of the above screenings was conducted two times to ensure reproducibility of results. Any primer which did not produce the same results was not used. Ultimately, 11 RAPD and 8 ISSR primers were selected for this study.

### Data Analysis

#### *ISSR and RAPD analyses*

Of 80 samples from which DNA was extracted, 74 accessions were ultimately included in all RAPD and ISSR data analyses. Five accessions with divergent band patterns were determined to be from a different *Senecio* species as at the time of sample tissue collection it was not possible to differentiate this second species of *Senecio*. These were dropped from further analyses. One accession was lost during DNA extraction.

Fifty-eight RAPD and seventy-five ISSR polymorphic markers were produced by PCR. Analysis showed that 28 markers had band patterns identical to other markers; these duplicates were dropped from further analysis. The remaining 42 RAPD and 63 ISSR markers were used in multivariate analyses of inter-individual and population genetic distance. For comparative data analyses of each marker type, a sub-sample of 35 markers of each type (for a total of 70) were randomly selected to provide an equal number of markers.

#### *Cluster analysis*

Matrices of RAPD and ISSR phenotypes, in which marker presence (1) or absence (0) was recorded, were analyzed for inter-individual genetic distance separately and together using the Euclidean distance coefficient of the SIMINT subprogram of NTSYS-pc, version 2.01d (Rohlf 1993). Resulting genetic distance matrices were used to construct dendrograms using the SAHN subprogram and employing unweighted pair group averaging (UPGMA) in NTSYS-pc.

#### *AMOVA*

Analysis of molecular variance (AMOVA) (Excoffier et al. 1992) was used to partition the genetic distance (assessed using Euclidean distance) among individuals within a population and among populations. This hierarchical analysis of variance partitions the total variance into covariance components (Schneider et al. 2000). The covariance components are used to compute fixation indices in terms of inbreeding coefficients (Schneider et al. 2000). AMOVA was originally developed for RFLP haplotypes, but has been used for RAPD phenotypes (Huff et al. 1993). By extension, it is also appropriate for ISSR phenotypes. The  $F_{ST}$  statistic was computed and tested for significance after 1000 permutations (Schneider et al. 2000). These analyses were undertaken using Arlequin ver. 2.0 (Schneider et al. 2000) available at <http://lgb.unige.ch/arlequin/software/>.

#### *Mantel test*

A Mantel test (Mantel 1967) of the correlation between genetic distances and geographic distances, and the correlation between the RAPD and ISSR genetic distance matrices were calculated for all

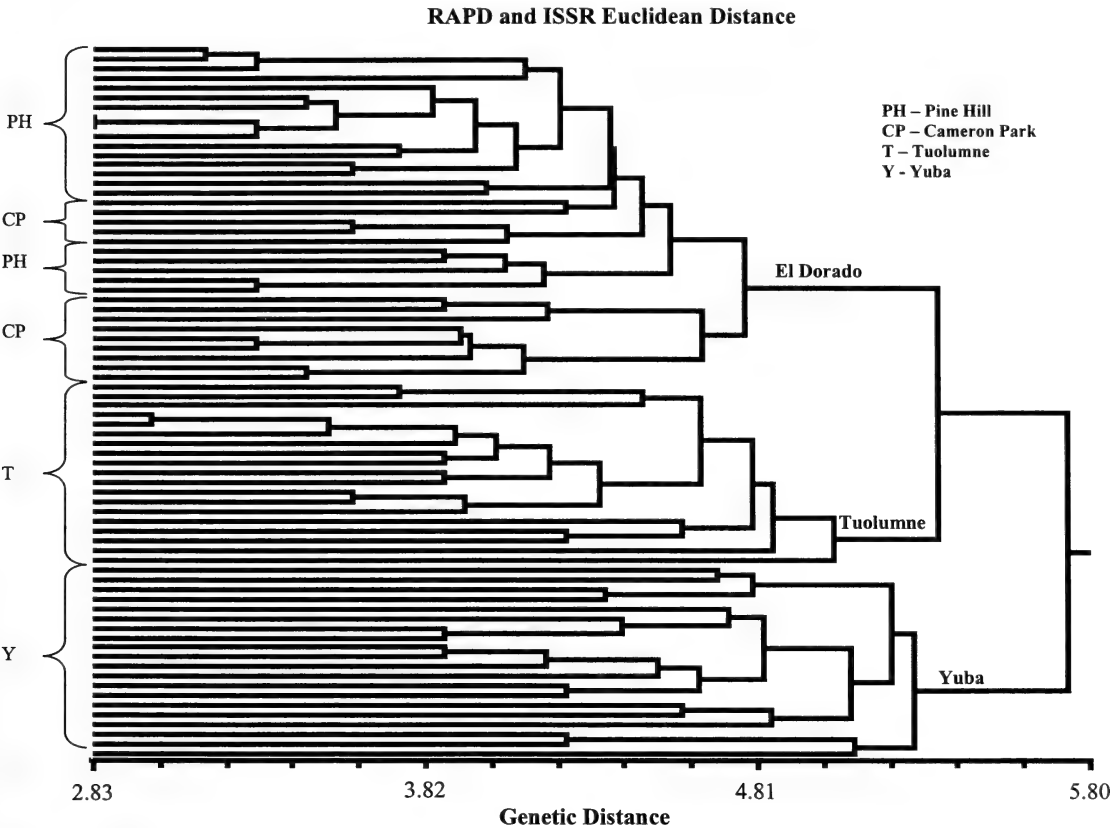


FIG. 2. UPGMA clustering of genetic distance of *Senecio layneae* individuals collected from Pine Hill (PH) and Cameron Park (CP) in El Dorado County, Tuolumne County (T), and Yuba County (Y).

pairs of individuals using the MXCOMP program in NTSYS-pc (Rohlf 1993). The significance of the matrix was evaluated by comparing the observed Mantel test statistic *Z*, with its random distribution obtained after 1000 permutations. Interindividual geographical distances were found by calculating the Euclidean distance based on the UTM coordinates of each population.

RESULTS

Eleven RAPD primers and eight ISSR primers produced 42 and 63 distinct polymorphic bands, respectively. ISSR's produced almost 2-fold more polymorphic bands per primer than RAPD's ( $P(t \geq 4.125) > 0.001$ ). Polymorphic bands ranged in size from 400 bp to 1800 bp.

Genetic Structure of *Senecio Laynea*

Multivariate analysis resulted in a dendrogram clearly showing three population clusters with all individuals grouped within their geographical populations at the county level (Fig. 2). While the El Dorado county populations of Pine Hill and Cameron Park were placed in a single large cluster, most

individuals were grouped into generally discrete subclusters within the main county cluster (Fig. 2). Highly significant ( $P < 0.000001$ ) genetic differences between populations were detected in the analysis of molecular variance (AMOVA) carried out on the genetic distance matrix. Of the total genetic diversity, 72% was attributable to individual differences within a population, and 28% to divergence among populations ( $F_{ST} = 0.28$ ) (Table 1). Analysis of just the two El Dorado County populations resulted in a  $F_{ST}$  of 0.22.

Analysis of Differences between RAPD and ISSR

Equalizing the number of polymorphic bands for each marker type and analyzing each marker type separately resulted in somewhat similar aggregations of individuals except for the Tuolumne County population. This population was genetically distinct when assayed by ISSR, but was intermixed with the Cameron Park and Pine Hill (El Dorado County) individuals when analyzed with RAPD markers (dendrogram not presented). The number of individuals placed in the wrong geographical population was significantly greater using RAPD's than ISSR's ( $0.01 < P(\chi^2 \geq 9.407) < 0.05$ ). An

TABLE 1. AMOVA OF GENETIC DISTANCE IN *SENECIO LAYNEAE*. The total data set contained 74 individuals from four populations; El Dorado County analysis includes two populations from that county. P is the probability of obtaining a larger than observed variance component or fixation index by chance alone.

Source of variation	Percentage of variation	P	Fixation indices
Among all populations	27.93	<0.001	F <sub>ST</sub> = 0.279
Within populations	72.07	<0.001	
Among El Dorado County pop's	21.59	<0.001	F <sub>ST</sub> = 0.216
Within El Dorado County pop's	67.29	<0.001	

AMOVA based on 35 ISSR markers resulted in a much stronger degree of between population differentiation than an AMOVA based on 35 RAPD markers ( $F_{ST} = 0.38$  and  $0.26$ , respectively).

#### Mantel Tests

The correlation between genetic distance (assessed using all markers) and geographical distance separating individual plants was not significant ( $r = 0.277$ ,  $P < 0.49$ ). The correlation between genetic distance matrices based on 42 RAPD markers and 63 ISSR markers was significant, but low ( $r = 0.345$ ,  $P < 0.002$ ).

#### DISCUSSION

Significant genetic structure exists in *S. layneae* ( $F_{ST} = 0.28$ ) resulting in three distinct geographic populations in El Dorado, Tuolumne, and Yuba Counties. Further, significant genetic structure ( $F_{ST} = 0.22$ ) exists between two populations, separated by 5.5 km, in El Dorado County. These statistical findings were in agreement with multivariate cluster analysis. In contrast, in *Wyethia reticulata*, a clonal sunflower restricted to chaparral in El Dorado County, populations separated by as little as 500 m had a distinct genetic identity (Ayres and Ryan 1997). The lack of significant correlation between genetic distance and geographic distance in *S. layneae* could be interpreted in two ways: either gene flow is occurring among all populations and they are not isolated from each other, or populations have been isolated for a long enough time for independent divergence to have occurred through random processes or natural selection. Given the preceding evidence, which supports substantial population divergence, we conclude that gene flow is extremely rare among populations of *S. layneae*, and populations have diverged through random genetic drift or selection.

Several characteristics that may counter the development of genetic structure are known for *S. layneae*. *Senecio layneae* is primarily outcrossing with insect pollination (G. Marsh unpublished data and personal observation), disperses its seed on the wind, and has a perennial life history. Outcrossing generally reduces genetic structure and promotes higher genetic variation within populations. Wide seed dispersal prevents divergence among popula-

tions via small amounts of long-distance migration and promotes higher genetic variation within populations. Perennial life history, especially long life, reduces the effects of drift and increases the chances of migration, thus hindering divergence of populations and loss of genetic variation. (Loveless and Hamrick 1984; Hamrick and Godt 1989; Linhart and Grant 1996; Ayres and Ryan 1999). These factors may be responsible for the intermingling of individuals from the Pine Hill and Cameron Park populations in El Dorado County within a single cluster: gene flow between the two sites, 5.5 km apart, does occasionally occur. Small populations of plants, scattered between these two populations, may act as a genetic bridge allowing this gene flow to occur. However, the species dispersal abilities do not extend to populations more than 90 km apart. The Red Hills Management Area sample site is approximately 98 km south of the Cameron Park sample site, and the Yuba County sample site is approximately 93 km north of the Cameron Park site. A comprehensive search for additional populations acting as genetic bridges between these three areas would shed more light on the patterns of genetic diversity in *S. layneae*.

Patchy spatial distribution can increase isolation and reduce gene flow, enhancing differentiation among populations if pollinator behavior reduces gene flow between patches. Patchy spatial distribution could also be at work in the apparent substructuring in the Pine Hill and Cameron Park populations. In addition, the ease and rapidity with which seeds of *S. layneae* germinate suggest that no seed bank exists, and so seed bank contributions probably do not play a role in the maintenance of within population diversity.

#### Utility of ISSR Markers

In this study, ISSR primers produced significantly more polymorphic bands per primer than did RAPD primers. More importantly, when equal numbers of polymorphic bands were used in cluster analysis of population membership patterns, ISSR-based genetic distance estimates more accurately portrayed population assignment of *S. layneae* individuals than RAPD-based estimates. Wolfe et al. (1998a) found that UPGMA dendrograms derived from ISSR markers showed more highly resolved

phylogenetic reconstructions of *Penstemon* populations in the section *Spectabilis* than trees based on rDNA, cpDNA, and allozyme identity coefficients. ISSR's better resolved genotypes for three of four populations studied than did RAPD's in examining clonal diversity in rare *Calamagrostis porteri* ssp. *inseperata* (Esselman et al. 1999). These results suggest a difference in the utility of RAPD and ISSR markers. In addition, the correlation between RAPD-based and ISSR-based genetic distance was low. These differences could arise due to differences in areas of the genome that each type of marker amplifies, because of higher error in RAPD markers, or because of higher precision in ISSR markers.

### Conservation Implications

One of the main goals of conservation programs for species that are rare or threatened is to maintain existing levels of genetic variation (Avice 1994). While most of the genetic variation in *Senecio layneae* is found within populations, almost  $\frac{1}{2}$  of variation is found among populations. This is enough to argue for conservation of *S. layneae* populations throughout its range. We also determined that populations separated by 5.5 km, while occasionally exchanging genes, are still quite distinct genetically ( $F_{ST} = 0.22$ ), which argues for the use of local seed (within 5.5 km) for restoration projects. The nature of the disjunct and patchy distribution of *S. layneae* populations is historical having to do with cycles of fire creating appropriate habitat within the chaparral. However, human activities, such as fire suppression and urban development, certainly influence habitat availability in El Dorado County extinguishing local populations and further isolating remaining populations. Information about the fate and persistence of *S. layneae* individuals and populations throughout a fire cycle will be necessary to formulate a conservation strategy for this species that goes beyond management of local populations in each of the counties where it is currently found.

Plants employ several mechanisms to cope with periodic fire. The responses to fire of three other rare plants found on the Pine Hill gabbro complex in El Dorado County demonstrate some of these strategies (D. Ayres unpublished data). Fire kills plants of the herbaceous trailing vine *Calystegia stebbinsii* but promotes seed germination from the soil seed bank. Plants grow rapidly and flower profusely 2–3 yr after fire. As the canopy closes during the interfire period *C. stebbinsii* almost completely dies out, but populations can once again establish after fire as long as the soil seed bank has been replenished. The fire response of the low growing woody shrub *Ceanothus roderickii* is quite similar, except that the juvenile plants do not begin to flower until 5–6 years after fire, and some plants survive and flower under mature chaparral. Populations require a fire-free period of at least 6 years to replen-

ish the seed bank in order to exist in perpetuity. Fire leaves unharmed the underground rhizomes of *W. reticulata* and promotes vigorous flowering and seed set. This plant remains in the understory in the interfire period when the canopy closes over, but with much reduced flowering vigor.

While we suspect that *S. layneae* does not have a fire resistant seed bank due to a relatively soft seed coat and an absence of any seed dormancy, this is but one of several questions regarding the fire response of *S. layneae* that needs to be addressed in order to formulate a management strategy for this species. Other questions concern the survival of the caudex during the interfire period and during fires, and the environmental conditions that promote flowering and favor seedling establishment. These biological constraints can be used to answer two key management questions; how long should the fire interval be, and how large should controlled burns be?

If the caudex of *S. layneae* can survive both the canopy closure of the interfire period, and fire, we predict it will respond similarly to *W. reticulata*; abundant flowering shoots will emerge from the caudex, seed production will be increased several fold, and seedlings will establish in the fire's ash. Under this scenario, precise fire intervals and areas are not critical management components for population survival as long as some areas burn sometime. However, if the caudex dies out during the interfire period or is killed by fire, and there is no seed bank, *S. layneae* will function as a fugitive species. It will require open patches of chaparral, near an existing reproducing population, to which the current crop of seeds can disperse and set seed before fire or canopy closure occurs. This is an entirely different fire survival strategy than the three other species described above and is similar to that of Furbish's lousewort (*Pedicularis furbishiae*) (Menges 1990). The disturbance/successional niche for Furbish's lousewort is defined by a river hydrology in which patches of dense shrub thickets and trees are removed by scouring ice flows and bank slumping. The lousewort recolonizes the newly opened patch from water-born seeds. In this model, disturbance in the form of fire or ice flows opens up the regeneration niche (Grubb 1977) allowing recolonization by wind or water-dispersed seed from surviving populations. Populations die out as succession progresses, so species survival requires ongoing disturbance. If this is the model for *S. layneae*, survival of the species will depend on both fire to create the regeneration niche and a supply of seeds to colonize the patch, either dispersing from neighboring populations, or from sown seed collected from nearby populations. Furthermore, the genetic structure found in *S. layneae* supports this 'fugitive' model where loss of populations due to catastrophic fires or lack of fires fragments populations and fosters genetic drift in the remaining populations.

Ideally, instead of focusing on the preservation of each extant population of each imperiled species as they occur today, the requirements for continued existence of all imperiled species will be incorporated into an integrated management plan. This plan would include fire management, control of invasive exotic plants, protection of preserve boundaries, prevention of short-interval fires, and strategies to ensure not only species survival but maintain patterns of genetic diversity laid down through millennia of microevolution.

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WOOD ANATOMY AND SUCCESSIVE CAMBIA IN *SIMMONDSIA*  
(SIMMONDSIACEAE): EVIDENCE FOR INCLUSION IN  
CARYOPHYLLALES S.L.

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ABSTRACT

*Simmondsia chinensis* (Link) Schneider, endemic to dry areas of California, Arizona, and adjacent Mexico, is the sole species of Simmondsiaceae. Wood anatomy and cambial activity of this species are analyzed in view of the transfer of the taxon from Buxaceae or Euphorbiales to Caryophyllales s.l. The wood contains features considered primitive in dicotyledons: tracheids, diffuse parenchyma, and rays that are both multiseriate and uniseriate. These features are shared with Agdestidaceae, Rhabdodendraceae, and Stegnospermataceae, families considered basal to most of the Caryophyllales s.s. (“core Caryophyllales”). *Simmondsia* has nonbordered perforation plates and successive cambia, features that occur widely in Caryophyllales s.l. Wood anatomy of *Simmondsia* is congruent with placement of the genus in Caryophyllales s.l. *Simmondsia* wood features reflect the desert habitat both quantitatively and qualitatively. Terminology and ontogenetic concepts of *Simmondsia* secondary xylem, successive cambial action, and periderm are contrasted with those in a previous study, and the problems of analysis of woods with cambial variants are discussed.

INTRODUCTION

*Simmondsia chinensis*, contrary to its species name, is native to limited areas of arid hills and low mountain ranges of southern California, southern Arizona and adjacent portions of Mexico (Munz 1973). The genus has frequently been placed in Euphorbiales (see Goldberg 1986, Table I, for the treatments of Simmondsiaceae by 11 leading phylogenists). Simmondsiaceae has been placed in the family Buxaceae within the order by many workers. The unisexual flowers and tricoccoid fruits were suggestive of this relationship for many systematists. However, *Simmondsia* was unique within Euphorbiales in having successive cambia. Successive cambia have evolved in several groups independently (e.g., Menispermaceae, Gnetales); consequently, the presence of successive cambia was probably not considered a feature of prime taxonomic value.

Recent phylogenies based on molecular data have opened possibilities in taxonomic interpretation with regard to *Simmondsia* and some other genera with successive cambia. These newer views have effectively supplanted earlier thinking, so various earlier phylogenies are not compared here. An expanded Caryophyllales (“caryophyllids”) was proposed by Williams et al. (1994). Most notably, Droseraceae and Nepenthaceae were added, with Dilleniaceae the first branch on this clade. In subsequent phylogenetic constructions (Nandi et al. 1998; Soltis et al. 2000), families added to the expanded Caryophyllales include Ancistrocladaceae, Asteropeiaceae, Dioncophyllaceae, Frankeniaceae, and Tamaricaceae. Santalales are considered the outgroup for Caryophyllales s.l. In all of the phy-

logenies utilizing molecular data, Buxaceae are not adjacent to Caryophyllales s.l., so the concept that *Simmondsia* belongs to Buxaceae is not supported.

The present study is designed to compare wood and stem anatomy of *Simmondsia* to that of Caryophyllales s.l. that may be related. That purpose was also basic to the recent study of Rhabdodendraceae (Carlquist 2001a). Successive cambia occur in Caryophyllales s.l. in Agdestidaceae, Amaranthaceae, Aizoaceae, Barbeuiaceae, Basellaceae, Caryophyllaceae, Chenopodiaceae, Nyctaginaceae, Phytolaccaceae, Plumbaginaceae, Polygonaceae, and Stegnospermataceae. The only families of Caryophyllales s.s. (“core Caryophyllales”) that lack successive cambia are Cactaceae, Didieriaceae, and Portulacaceae. Thus, the presence of successive cambia in *Simmondsia* alone is a reason to compare *Simmondsia* to Caryophyllales.

There have been previous accounts of *Simmondsia* wood, notably those of Solereder (1885, reported as *Brocchia*), Van Tieghem (1897), Bailey (1980), and Carlquist (1982a). The present study goes beyond those studies by utilizing scanning electron microscopy (SEM) and by careful attention to ontogenetic phenomena (and associated terminology). Better understanding of successive cambia in *Simmondsia* will lead to a more accurate picture of successive cambia in dicotyledons and Gnetales.

MATERIAL AND METHODS

Stems of *Simmondsia chinensis* from a large shrub cultivated in the Santa Barbara Botanic Garden were fixed in 50% aqueous ethanol. Stems were taken in January and June, 2001, in order to compare degree of meristematic activity in the lat-



eral meristem. The stem of *S. chinensis* is hard enough to be sectioned, without softening, on a sliding microtome, but thin sections contain fractures. Some sliding microtome sections were stained with safranin and used for permanent slides. Some tangential sliding microtome sections were dried between clean glass slides, sputter coated with gold, and viewed with a Bausch & Lomb Nanolab SEM. Portions of "bark" (tissue exterior to vascular bands) were fixed in 50% aqueous ethanol, softened for three days at 60°C in 8% ethylene diamine, infiltrated, embedded with paraffin, and sectioned according to the method of Carlquist (1982b). These sections were stained with a safranin-fast green combination. Macerations were prepared with Jeffrey's Fluid (equal parts of 10% chromic acid and 10% nitric acid) and stained with safranin. The stems studied were between one and three cm in diameter.

Vessel lumen diameter rather than outside vessel diameter was measured; for vessels oval in transection, long and short chords were averaged. The vessel density recorded was based upon scans that did not include conjunctive tissue. If conjunctive tissue were to be included, the number of vessels per mm<sup>2</sup> would be about 50% lower. Both earlywood and latewood were included in the computation of quantitative vessel data. Terms are in accordance with the IAWA Committee on Nomenclature (1964) and Carlquist (2001b). The term "successive cambia" follows the usage of Schenck (1893) and Pfeiffer (1926).

## RESULTS

### Secondary Xylem

Growth rings inconspicuous, but evident on the basis of earlywood vessel diameter (Fig. 1); earlywood is usually not initiated at the beginning of each vascular band, but at some point within vascular bands. Vessels are virtually all solitary (Fig. 1); mean number of vessels per group, 1.04. Mean vessel lumen diameter, 21 µm. Mean number of vessels per mm<sup>2</sup>, 260 µm. Mean vessel element length, 163 µm. Mean vessel wall thickness, 2.8 µm. Perforation plates simple, nonbordered (Fig. 3, top). Helical thickenings present on vessel walls, some in the form of pairs of thickenings paralleling helices of pits (Fig. 3). Pit cavities of lateral wall vessel pits about 3 µm in diameter. Imperforate tracheary elements all tracheids, densely covered with fully bordered circular pits about 3 µm in diameter (Fig. 4). Mean tracheid wall thickness, 3.2 µm. Axial parenchyma sparse, diffuse, composed of cells that are not subdivided. Rays uniseriate to wide multiseriate (Fig. 2); uniseriate rays are more common than multiseriate rays. Most uniseriate rays are a single cell in height (and thus not easily seen in Fig. 2). Mean height of multiseriate rays, 212 µm. Mean width of uniseriate rays, 74 µm. Mean ray cell wall thickness, 1.5 µm, walls lignified. Ray cell

wall pits simple. Ray cells predominantly procumbent; square and upright cells relatively uncommon. Starch abundant in ray cells (Fig. 5). Secondary xylem nonstoried.

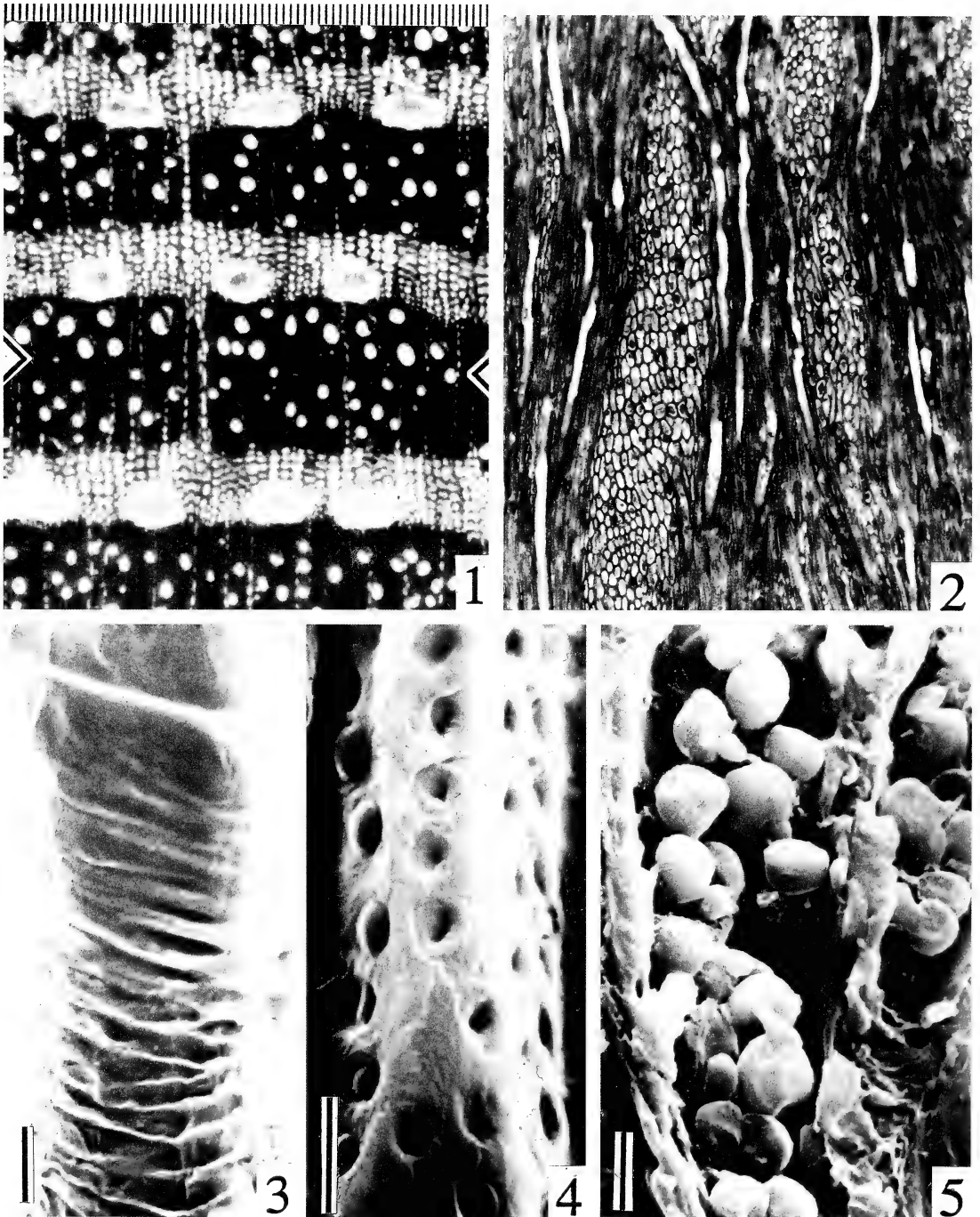
### Conjunctive Tissue and Cambial Action

Conjunctive tissue is composed of bands five to ten cells thick radially (Fig. 1: tangential bands of thin-walled radial cells, containing phloem strands, intervening between tangential bands of dark secondary xylem). As seen in radial section (Fig. 6), cells are mostly upright, a few square (and thus contrast with ray cells of the secondary xylem). Cell walls of conjunctive tissue are lignified and about 1.5 µm in thickness, but thin-walled nonlignified cells present on bark side of phloem strands (Fig. 7, above crushed phloem). Functional phloem cells, adaxial to the dense crushed phloem strand, are somewhat compressed due to sectioning rather than polygonal. What portion of the phloem cells that are not crushed are functional could not be determined. Continued production of secondary phloem is possible because earlier-formed phloem is progressively crushed. Solitary rhomboidal crystals are occasional in conjunctive tissue (Figs. 6, 8). Periclinal divisions can be seen in young conjunctive tissue (Fig. 9), but number of cell layers in the meristematic zone of the lateral meristem between the most recently initiated vascular cambium and the previous vascular band varies (e.g., Fig. 8).

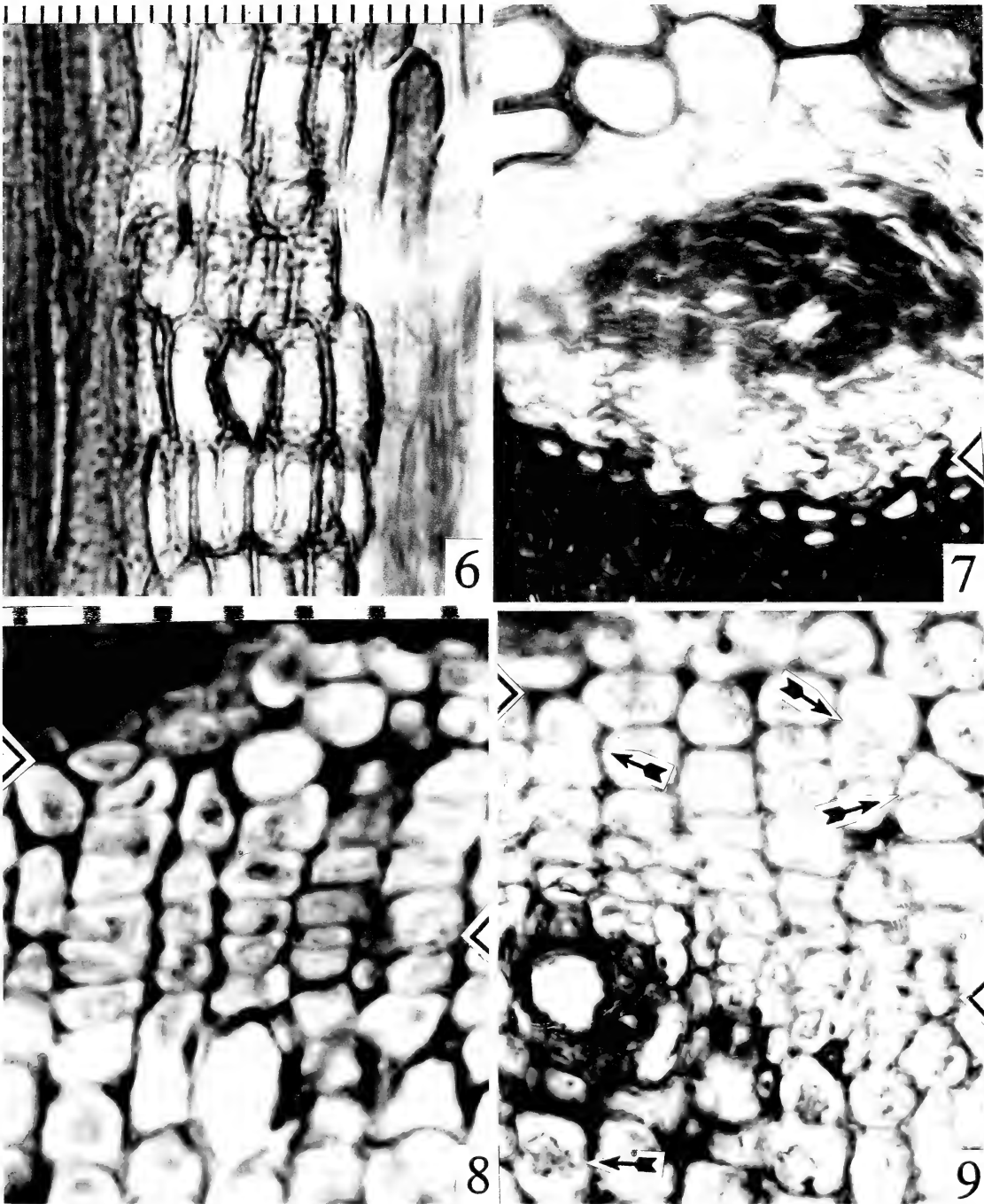
Vascular cambia (pointers at right edge, Figs. 7–9) actively produce secondary phloem and secondary xylem: the secondary phloem occurs as isolated strands, whereas the secondary xylem mostly occurs as unbroken cylinders that extend around the stem. The first tracheids produced by a cambium are polygonal in outline, and their alignment in radial rows is sometimes obscure because during maturation, the interfaces of the several faces shift. As divisions wane in each vascular cambium, a few thin-walled tracheids in radial rows are produced (Fig. 7, below phloem). Cambial activity produces phloem for a prolonged period, probably for several years because the abaxial portion of secondary phloem strands consist of numerous crushed phloem cells (Fig. 7, gray mass in center of photograph) and phloem cells produced by the cambium are in radial rows. Also, crushed phloem cells are always abaxial to apparently functional secondary phloem cells (Figs. 1, 7).

### Phellogen and Lateral Meristem Action

The outer layers of the relatively mature stems studied here lack the cortical fiber strands reported by Bailey (1980) in the relatively young stems he studied. Such fiber strands had been shed from the stem I studied. Phellem, which consists of cells filled with dark-colored contents, is present on the stem surface. The phellem cells are narrower than cells in what is here termed diffuse lateral meristem



FIGS. 1-5. Stem sections of *Simmondsia chinensis*. 1. Transection (abaxial side above), showing alternation of bands of secondary xylem (each with associated phloem strands) and conjunctive tissue; vascular bands are not annual in extent; the pointers demarcate part of the earlywood of one year (above pointers) from part of the latewood of the preceding year (below pointers), several vascular bands are produced per year. 2. Tangential section of secondary xylem; a few large multiseriate rays are apparent (center), uniseriate rays are mostly inconspicuous because of their very small size. 3-5. SEM photographs from a tangential section of secondary xylem. 3. Portion of inner surface of a vessel, showing nonbordered perforation plate (top) and helical thickenings. 4. Outer surface of a tracheid, showing bordered nature and density of pits. 5. Starch grains in ray cells. Figs. 1, 2, magnification scale above Fig. 1 (divisions = 10  $\mu$ m; Figs. 3-5, scale bar in each figure = 5  $\mu$ m).



FIGS. 6–9. Sections of stem of *Simmondsia chinensis*. 6. Radial section of conjunctive tissue to show cell shape and (center) rhomboidal crystal (secondary xylem at extreme left, secondary phloem at extreme right). 7. Strand of secondary phloem and surrounding tissues (conjunctive tissue above, secondary xylem below); crushed secondary phloem in abaxial part of phloem strand (pointer indicates site where vascular cambium was prior to cessation of active division). 8, 9. Transverse sections of lateral meristem zone at periphery of stem; pointers at left in each indicate offset between outermost cells of the radial lateral meristem (radial files) and the innermost periderm cells; pointers at right indicate vascular cambium location. 8. Lateral meristem zone in which a vascular cambium has recently formed (no secondary xylem or phloem elements identifiable yet); rhomboidal crystal at bottom center. 9. Lateral meristem zone in which vascular cambium has yielded a vessel (extreme left) and some tracheids as well as some secondary phloem (right). Diagonal arrows denote recent divisions in the radial files of the lateral meristem zone; horizontal arrow (lower right) denotes a cell plate (obscured by cell contents adherent to it) that indicates a recent division in conjunctive tissue that is still somewhat meristematic. Figs. 6, 7, magnification scale above Fig. 6 (divisions = 10  $\mu$ m). Figs. 8, 9, scale above Fig. 8 (divisions = 10  $\mu$ m).

(it could also conceivably be termed secondary parenchyma). The diffuse lateral meristem cells are in radial rows; the term "diffuse" is used because divisions do not occur synchronously in a single layer as in a vascular cambium, but are randomly distributed throughout the meristematic zone (see Carlquist 1999a). A lateral meristem that consists of a single layer was observed in *Barbeuia* (Carlquist 1999b) and also occurs in Nyctaginaceae (Carlquist unpublished data; data in earlier papers vary in interpretation and will be discussed in a later paper). More numerous divisions were observed in the stems collected in June than in those collected in January. The radial rows of lateral meristem cells are offset from the periderm which consists of a single layer of phellogen (narrow, like the phellem cells, but devoid of dark-colored compounds). In some places, there is a layer of parenchyma between the phellogen and the lateral meristem files. No phellogen cells were identified unequivocally. The offset between the radial rows of the diffuse lateral meristem and the periderm is indicated by a pointer at the left in Fig. 8 and Fig. 9. The entirety of the periderm is illustrated in Figs. 8 and 9, which were selected to show primarily lateral meristem and vascular cambia.

Origin of vascular cambia occurs within the radial files of cells produced by the diffuse lateral meristem. Although only a small portion (for reasons of clarity) could be illustrated, study of the entirety of sections validates this interpretation. The origin of a vascular cambium (Fig. 8, pointer at right) can be distinguished from divisions of the lateral meristem because divisions of the vascular cambium form a single meristematic layer of divisions that are synchronous in tangential bands around the stem. Each vascular cambium soon produces secondary xylem internally (adaxially) and secondary phloem abaxially (Fig. 9, pointer at left; vessels and a few tracheids in secondary xylem). The terminal products of a vascular cambium (Fig. 7) are described above.

## CONCLUSIONS

### Phylogenetic Position

The occurrence of successive cambia is a character widespread in Caryophyllales s.s. ("core Caryophyllales") so its occurrence in families now added to an expanded Caryophyllales-Rhabdodendraceae (Carlquist 2001a) and Simmondsiaceae is not surprising. "Caryophyllales: s.s." corresponds to the betalain-containing families plus Achatocarpaceae, Barbeuiaceae, and Molluginaceae, and the genera *Limeum* and *Lophiocarpus* (Clement et al. 1994). *Simmondsia* has characters generally considered primitive in dicotyledons: presence of tracheids, presence of diffuse axial parenchyma, and presence of both multiserial and uniserial rays (Metcalf and Chalk 1950: xlv, "fibres with distinctly bordered pits;" Kribs 1935, 1937). All of

these features are present in Rhabdodendraceae (Carlquist 2001a), now placed at the base of Caryophyllales s.l., and in genera now placed at or near the base of Caryophyllales s.l. (Soltis et al. 2000). *Simmondsia* is placed by Hoot et al. (1999) and Soltis et al. (2000) near the base of Caryophyllales s.s. The other genera with the primitive features listed above include *Agdestis* (Carlquist 1999c) and *Stegnospema* (Carlquist 1999a); *Barbeuia* has tracheids, but not the other character states mentioned above (Carlquist 1999b).

One feature of possible ordinal significance is the presence of nonbordered perforation plates. These have been demonstrated in most Caryophyllales s.s. (see Carlquist 1999a, b, 2000). Nonbordered perforation plates are newly reported here for *Simmondsia* (Fig. 3), and have recently been reported for some Caryophyllales s.l. such as Rhabdodendraceae (Carlquist 2001a). Nonbordered perforation plates may be a symplesiomorphy in Caryophyllales s.l. according to the above data and other observations (Carlquist 2001b).

### Ecology

*Simmondsia* is a desert shrub with only slight succulence in the leaves (Bailey 1980); not surprisingly, it has xeromorphic wood. The Mesomorphy Ratio (vessel diameter times vessel element length divided by vessel diameter) was reported to be 27.8 for *Simmondsia* by Carlquist and Hoekman (1985). A very similar value (24.4) can be derived from the present data if conjunctive tissue is not excluded. The similarity of the two reports is even closer if one notes that outside vessel diameter, rather than lumen diameter was used by Carlquist and Hoekman (1985).

Tracheids are conductively safe (excellent at confining embolisms to a single cell) compared to vessel elements. Fiber-tracheids and libriform fibers, by contrast, are nonconductive (see discussion in Carlquist 2001b). The presence of tracheids in *Simmondsia* is a feature of value in a xeromorphic habitat. Because of the presence of tracheids, vessel grouping in *Simmondsia* is virtually nil (1.04), in agreement with the correlation for dicotyledons as a whole claimed by Carlquist (1984). The value of tracheids in promoting conductive safety exceeds the value of vessel grouping (Carlquist 2001b).

### Ontogeny and Terminology

The terminology in papers and books that deal with successive cambia is remarkably diverse, but more significantly, different interpretations often underlie the terms used. The present paper is not a proper venue for a review of this situation. However, the paper by Bailey (1980) on *Simmondsia* is appropriate for comparison in view of the ontogenetic interpretations as well as mature structures detailed in both the present paper and Bailey's.

In the present interpretation, a diffuse lateral

meristem forms outside of the vascular cylinder, near the stem periphery. This lateral meristem produces radial files of cells, producing parenchyma cells with primary walls, cells which remain relatively meristematic judging from recent divisions to be found in this region. Within the lateral meristem zone, a new vascular cambium is formed (usually while the preceding vascular cambium is still actively producing secondary xylem and phloem). In Bailey's (1980) interpretation, the zone I have termed lateral meristem is called conjunctive tissue (despite its lack of lignified secondary walls as found in conjunctive tissue in older parts of the stem). Bailey (1980) uses the term "extrafascicular cambium" for what I term the vascular cambium in each of the concentric vascular bands.

Bailey (1980) claims that "the phellogen is actually a region of transition where the peripheral conjunctive parenchyma of previous extrafascicular cambia undergoes further cellular subdivision; a true phellogen is lacking." In the relatively young stems illustrated by Bailey (1980), phellogen might well be formed from cortical parenchyma as it is in many dicotyledons, but my studies indicate the existence of a self-perpetuating phellogen, as so frequently described in dicotyledons. This phellogen is distinguished from the lateral meristem (outermost conjunctive parenchyma of Bailey) not only by its tangentially narrower cell diameter but by an offset between the periderm files and the files of cells in the radial parenchyma (Figs. 8, 9). These two differences would be difficult to explain if periderm were ontogenetically continuous with the files of cells of the lateral meristem.

The vascular cambia produce strands of secondary phloem externally and cylinders of secondary xylem internally. In my interpretation, quite ordinary rays are produced by each cambium. In Bailey's (1980) interpretation, "conjunctive tissue initials produce raylike structures of conjunctive tissue; true vascular rays are absent." This interpretation has not, to the best of my knowledge, been offered in any genera with successive cambia other than in Bailey's study of *Simmondsia*.

The differences in interpretation detailed above show that careful analyses of successive cambia and other cambial variants still need to be undertaken. The diversity of interpretations and terms for the anatomical phenomena is still considerable. The number of different interpretations and terms within instances of successive cambium occurrence seems unlikely to be matched by an equal diversity of ontogenetic mechanisms. Rather, cellular arrangements have been viewed differently by different workers. In part, the diversity of interpretations and terminology may derive from microtechnical considerations. Thin sections such as can be cut with a rotary microtome, are desirable for revealing cell lineages and histological details clearly. The hardness of many stems with successive cambia has, on the contrary, led to preparation of sliding micro-

tome sections in which soft tissues do not section well or are too thick for cell development sequences to be revealed clearly. The use of rotary microtome sections of material that has been chemically softened to a suitable degree seems the best solution to this dilemma. Embedding in resin or plastic is an alternative microtechnical possibility.

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A NEW SUBSPECIES OF *NAVARRETIA LEUCOCEPHALA*  
(POLEMONIACEAE) FROM VERNAL POOLS IN EASTERN WASHINGTON

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ABSTRACT

*Navarretia leucocephala* Benth. subsp. *diffusa* is newly described from numerous populations in a distinctive vernal pool landscape in the Channeled Scablands of Eastern Washington. Its affinities appear closer to subspecies of *N. leucocephala* in the California floristic province, than subspecies *minima*, which is the only other member of the *N. leucocephala* group known to grow within the range of the Flora of the Pacific Northwest (Hitchcock and Cronquist 1973). The range of subspecies *diffusa* closely corresponds with the central of three channels of the glacial Spokane Flood events and is segregated from populations of subspecies *minima* by expansive Palouse loess uplands, where vernal pools are absent. Just as no plants of subspecies *diffusa* were found outside this central flood channel, no plants of subspecies *minima* were found within the range of subsp. *diffusa*. Plants of *N. leucocephala* subsp. *diffusa* are easily distinguished from subspecies *minima* in Washington by the fewer flowers within the much more openly diffuse heads, and by the conspicuously puberulent calices, fewer seeds per capsule, longer corolla lobes and higher filament insertion. It is distinguished from other subspecies by the consistently puberulent calices, low seed number and the relatively simple outer inflorescence bracts.

Key words: *Navarretia*, Polemoniaceae, vernal pools, Columbia Plateau, Channeled Scablands

The *Navarretia leucocephala* Benth. complex includes four species in North America: *N. fossalis* Moran, *N. leucocephala* Benth, *N. myersii* P.S. Allen & A. G. Day (two subspecies) and *N. prostrata* (A. Gray) E. Greene, and one in South America: *N. involucreta* Ruiz & Pavón (Day 1993a). *Navarretia leucocephala* is defined as having five subspecies: *leucocephala*, *bakeri* (H. Mason) A. G. Day, *minima* (Nuttall) A. G. Day, *pauciflora* (H. Mason) A. G. Day, and *plieantha* (H. Mason) A. G. Day (Day 1993a). Two of the subspecies are widespread; subspecies *leucocephala* occurs in the Great Valley of California and in southwestern Oregon (Day 1993b), and subspecies *minima* is found from California to north-central Washington, western Idaho and to Utah. During a study of vernal pools of the Columbia Plateau, populations of *Navarretia leucocephala* encountered in one subregion of the Columbia Plateau vernal pool province stood out as being highly distinctive, leading to the morphological comparison with the other subspecies of *N. leucocephala* presented here.

TAXONOMY

***Navarretia leucocephala* Benth. subsp. *diffusa***  
Björk subsp. nov.—TYPE: USA, Washington State, Lincoln County, Swanson Lakes Wildlife Management Area. Floors of vernal pools on scabland basalt flows. 680 m. T24N R34E S4 NE/4. June 18, 1997 Curtis R. Björk 3229 (Holotype, WS, Isotype WTU).

Planta annua, erecta vel decumbens, 0.5–4.7 cm lata; caulis centralis 1.0–13.4 cm alta, ad medium

0.3–0.7 mm crassus; capitula hemispherica, (1) 4–10 (15) mm lata, diffusa, plerumque ramificans, floribus (1) 5–20 (30); bractae exteriores lobis (0) 2–6 (8); calyx pilis brevis crispis plerumque recurvatis, lobi plerumque integri; corolla inclusa, alba, lobi lineares; stamina in sinibus loborum corollam inserta, inclusa, stigma superantibus; semina (1) 2 (3).

Plants annual, erect to decumbent, 0.5–4.7 cm wide; central stem 1.0–13.4 cm high,  $0.6 \pm 0.1$  mm thick at midlength; heads hemispheric, (1) 4–10 (15) mm wide, diffuse and generally branching, with (1) 5–20 (30) flowers; outer bract lobes (0) 2–6 (8); calyx conspicuously puberulent with crisped, mostly recurved hairs, lobes mostly entire; corolla included, white, lobes linear; stamens included, inserted near corolla-lobe sinuses, surpassing the stigma; seeds (1) 2 (3).

*Paratypes.* U.S.A. Washington, Lincoln County: adjacent to Knack Road, 3.5 miles SSW of Telford, T25N R35E S29 NE ¼ of NW ¼, Björk 3228 (WS), 18 June 1997; Swanson Lakes Wildlife Management Area, 1 mile West of Florence Lake, June, 1999, Björk s.n. (WS); Swanson Lakes Wildlife Management Area, 2 miles East of refuge headquarters, T25N R34E S35 NE ¼, 19 June 1997, Björk 3250 (WS); 3.4 miles SSE of Swanson Lakes, along Seven Springs Dairy Road, 13 June, 1998, Mark Fishbein 3439 (WS); Large vernal pool along Swanson Schoolhouse Road, T25N R34E S31 NW ¼ of NW ¼, Björk 6161 (WS).

*Comparative morphology.* Plants of this distinctive group of populations are here named *Navarretia leucocephala* subspecies *diffusa* and are clear-

ly distinguished from all other subspecies of *N. leucocephala* by their consistently and conspicuously puberulent calyx, their generally much more diffuse heads and their relatively simple outer bracts (Table 1). It is placed within *N. leucocephala* rather than with any other species or in its own specific rank due to the similarity of plant architecture and the cymose inflorescence to those of subspecies *N. leucocephala* (in contrast especially to *N. myrsii* and *N. prostrata*) (Crampton 1954), and due to the low seed number (in contrast with *N. fossalis*). Additionally, it differs from the South American species *N. involucrata* by flower color and the simpler leaves and bracts. The subspecies of *N. leucocephala* with the greatest morphological similarity to subsp. *diffusa* appears to be subsp. *pauciflora* of Northern California. Both have few seeds per capsule (usually 2 in both subspecies), few flowers per head, high filament insertion and corollas with narrow throats and linear lobes. Specimens of subspecies *diffusa* are distinguished from those of subspecies *pauciflora* by the often broader (to 15 mm, though still few-flowered) and more diffuse heads, the consistently white flowers (versus the generally bluish flowers of subspecies *pauciflora*), the simpler outer bracts and the taller stature (central stem length to 10 cm). Also similar to subspecies *diffusa* is subspecies *bakeri* of Northern California and Southwestern Oregon. The fewer flowers per head and fewer seeds per capsule distinguish subsp. *diffusa* from subsp. *bakeri*. Subspecies *diffusa* differs from subsp. *leucocephala* in the included corollas and the higher filament insertion. Subspecies *diffusa* is distinguished from subsp. *plieantha* by the white versus bluish flowers, fewer flowers per head and by the lower seed number.

Subspecies *diffusa* differs from subsp. *minima* by the simpler bracts, fewer flowers per head, lower seed number, lesser central stem length and width, narrower head width, higher filament insertion, calyx length and the fewer calyx lobe divisions (Table 2). Plants of subspecies *diffusa* are also distinguished from subsp. *minima* by the nearly simultaneous maturation of flowers within a head. Unlike in subsp. *diffusa*, there are typically some flowers in subsp. *minima* heads that bear mature seeds while others are not yet in anthesis. The heads of subsp. *diffusa* are openly branching, so much so that the calyx bases are often clearly seen within. The calyx lobes of subsp. *diffusa* are unequal and longer in relation to the tube, ranging from 0.8–1.5 × the tube length, in contrast to those of subsp. *minima*, which are usually subequal in length and 0.5–1.0 × the tube length. Additionally, one to three of the ribs leading to the lobes in subsp. *diffusa* maintain their width and herbaceous tissue to the base of the calyx tube. The ribs are often wider than the intervening membranes, which is apparently unique within section *Navarretia* (Day 1993b) and the *N. leucocephala* complex. The calyx tube in subsp. *diffusa* is conspicuously puberulent

TABLE 1. MORPHOLOGICAL COMPARISONS OF THE SUBSPECIES OF NAVARRETIA LEUCOCEPHALA AND N. L. SUBSP. DIFFUSA SUBSP. NOV. Outlier values are shown in parentheses. Data are in part from Day 1993b, with additional observations from herbarium specimens (WS, OSC).

	<i>leucocephala</i>	<i>minima</i>	<i>bakeri</i>	<i>plieantha</i>	<i>pauciflora</i>	<i>diffusa</i>
Central stem length (cm)	2–22	2–11	2–10	1–3	1–4	1–16 (10)
Head width (mm)	9–36	(4) 7–16 (20)	13–24	15–20	6–12	(1) 4–10 (15)
Flowers per head	15–80	20–80	30–60	20–80	6–30	(1) 5–20 (30)
Outer bract lobes	4–14	4–10	9–16	6–10	4–12	(0) 2–6 (8)
Bract lobe 2° divisions	(0) 4–19	(0) 4–16 (30)	8–30	4–8	0–10	0–6
Bract length/head width ratio	1.5–3.0×	1.5–3.0×	1.2–2.5×	1.0–2.0×	1.7–3.5×	1.0–2.2×
Calyx tube/lobe length ratio	0.6–3.0×	1.0–2.0×	1.0–2.3×		0.8–3.0×	1.5–3.0×
Calyx lobe relative lengths	gen. ± equal	gen. unequal	gen. ± equal		gen. ± equal	gen. ± equal
Calyx lobes divided	gen. none	(1) 2–3	none	gen. sparse	none	gen. none
Calyx pubescence	gen. sparse	gen. sparse	gen. sparse	gen. bluish	gen. sparse	dense
Corolla color	white	white	gen. white	gen. bluish	gen. bluish	white
Corolla lobe shape	± ovate	± oblong	± linear	± linear	± linear	± linear
Corollas included/exserted	excl.	incl.	incl.	incl.	incl.	incl.
Filament insertion	in throat	in throat	at sinuses	at sinuses	at sinuses	at sinuses
Seed number	4–7	(2) 3–5 (6)	2–4	2–3	2	1–2 (3)



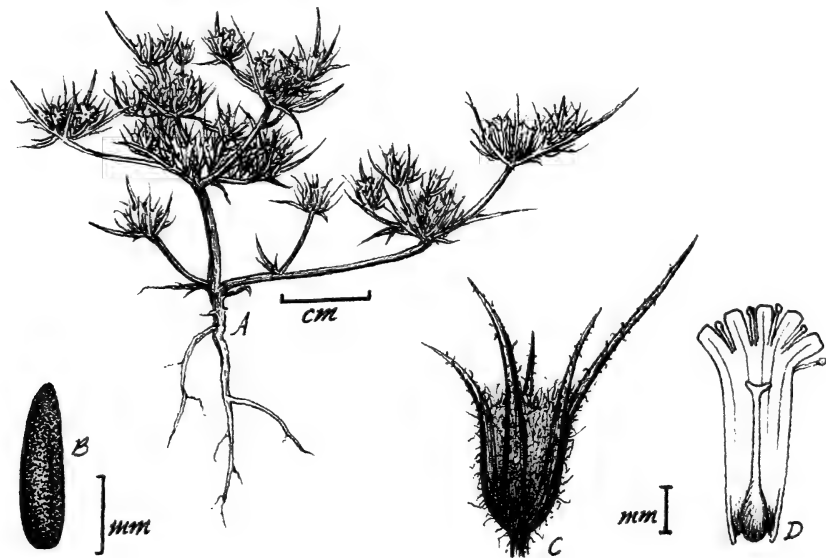


FIG. 1. Illustration of *Navarretia leucocephala* subsp. *diffusa*. A. Mature plant in anthesis. B. View of a seed, showing slightly roughened surface. C. Side view of a calyx. D. Corolla, opened from the side and showing pistil and relative positions of anthers and stigma. Note also the single veins entering the corolla lobes.

throughout with crisped, usually recurved hairs. The mouth of the calyx is less strongly pubescent in subsp. *diffusa*, despite the external pubescence, than in subsp. *minima*, and the hairs are shorter and thinner in width. The corolla lobes of subsp. *diffusa* are narrower and less rounded at the apex than in subsp. *minima*. Subsp. *diffusa* has simpler leaves, often lacking lobes. The stems of subsp. *diffusa* are typically reddish, which is not usually the case with subsp. *minima*, and the stem pubescence differs from subsp. *minima* in being sparser, more crisped and less strongly recurved. Additionally, subsp. *diffusa* stems often bear scattered patches of glandular hairs. These differences are consistent throughout the ranges of both subspecies, and no obvious intermediates were found.

*Ecology and distribution.* The range of subsp. *diffusa* closely corresponds to a broad, basin-like expanse of basalt flows surrounded by loess hills to the east and west, and sand and gravel deposits to the south. This basin was formed by massive floods during the last ice age. The repeated sudden failure of an ice-dam in Montana released enormous amounts of water onto the Columbia Plateau, scouring away the thick loess deposits and exposing the basalt bedrock over large areas (Bretz 1969). The flood waters gouged out three main channels, and it is the central of the three, in an area of approximately 550 km<sup>2</sup> where subsp. *diffusa* is found to the exclusion of subsp. *minima*. Other vernal pool landscapes occupy the eastern and western of the three flood channels. There, subsp. *minima* grows

TABLE 2. QUANTITATIVE MORPHOLOGICAL COMPARISONS BETWEEN SUBSP. MINIMA AND SUBSP. DIFFUSA. Means are given with one standard error and were tested on the null hypothesis of no difference in one-way ANOVAs. Measurements were taken from 50 plants of subsp. *minima* collected from 7 locations in Spokane, Adams, Klickitat and southwest Lincoln counties, and 60 plants of subsp. *diffusa* collected from 5 vernal pools in two locations in central Lincoln County. Asterisks indicate statistical significance (\*\* p < 0.01; \*\*\* p < 0.001).

	Subsp. <i>minima</i>	Subsp. <i>diffusa</i>
Plant width (cm)	4.6 ± 0.6	3.5 ± 0.4
Central stem length (cm)	6.5 ± 0.4	4.0 ± 0.3***
Central stem width (mm)	0.8 ± 0.1	0.6 ± 0.1***
Heads per plant	7.3 ± 1.0	4.9 ± 0.6
Head width	11.2 ± 0.3	7.0 ± 0.3***
Flowers per head	23.3 ± 1.6	10.1 ± 0.8***
Outer bract divisions	7.4 ± 0.4	4.5 ± 0.2***
Calyx length	5.5 ± 0.1	4.8 ± 0.1**

in the absence of subsp. *diffusa*. Thus, the two subspecies of *Navarretia leucocephala* in Washington are geographically isolated from each other by the loess hills, possibly leading to genetic isolation.

*Navarretia leucocephala* subsp. *diffusa* is found exclusively in vernal pool basins like all the members of the *N. leucocephala* group (Spencer 1997). It is submerged at germination (in early to mid spring on the Columbia Plateau) and it grows and flowers when emergent (late April to early July during normal years). Subspecies *diffusa* is abundant in many hundreds of vernal pools, from those as small as 1 m<sup>2</sup> and no deeper than 1 dm to those as wide as 50,000 m<sup>2</sup> occupying basins as deep as 1 m. The plants were never found along intermittent streams or in any other wetland type. The greatest density of individuals is usually where there is little competition from taller plants, though high densities are sometimes found under dense canopies of *Deschampsia danthonioides* (L.) Beauv. on pool margins. Common associates are *Polygonum polygaloides* subsp., *Psilocarphus* spp., *Bousiduvalia* spp., *Alopecurus saccatus* Vasey and *Downingia yina* Applegate. Surrounding plant communities are complex and highly diverse mosaics of numerous shrub, forb and graminoid codominants on lithosol, mima mounds and wetland soils.

No major ecological differences were apparent between the sites in which subsp. *diffusa* and subsp. *minima* occurred in Washington. However, in casual observations, a difference was noted in drought response among the taxa that may be significant. Despite the similarly dry and hot conditions of the ranges of subspecies *diffusa* and *minima*, plants of subsp. *diffusa* were more able to withstand the drought and produce seed than plants of

subsp. *minima*. A large proportion of the seedlings of subsp. *minima* died during an early three-week drought and high temperatures in April, 1998, while very few drought-killed individuals of subsp. *diffusa* were seen until late June of that year.

#### ACKNOWLEDGMENTS

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## RESURRECTION OF A CENTURY-OLD SPECIES DISTINCTION IN *CALAMAGROSTIS*

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### ABSTRACT

We investigated genetic diversity and taxonomic status within *Calamagrostis breweri* Thurber *s. l.*, a rare alpine grass species comprising two allopatric races apparently differing in chromosome number. We analyzed isozymes and morphology of both races. The two races differ in leaf width and involution, leaf vein number, certain morphometric characters of the inflorescence, and habitat. Isozyme band patterns also distinguished the northern and southern forms, and revealed little variation within populations. Because the northern and southern forms are genetically, ecologically, and morphologically distinct and apparently differ in chromosome number, they should be distinguished taxonomically as separate species. The southern form is here named *C. muiriana* sp. nov. in honor of John Muir, whose writings played an important role in the conservation of *C. muiriana* habitats. The name *Calamagrostis breweri* Thurber is retained for the northern form.

Key words: *Calamagrostis breweri*, grass, polyploidy, isozymes, *Calamagrostis muiriana* sp. nov., rare, alpine, Poaceae

The name *Calamagrostis breweri* Thurber is applied to two small, glaucous, subalpine grasses that differ in chromosome number, isozymes, range, ecology, leaf anatomy, and details of morphology. The diversity within *C. breweri sensu lato*, has been discovered repeatedly (Kearney 1898; Nygren 1954; S. Nugent personal communication; G. L. Stebbins personal communication to C. W. Greene). The one previous attempt to segregate the populations nomenclaturally (Kearney 1898) foundered on a misinterpretation of type specimens and gave the northern taxon two names (*C. breweri* and *C. lemmoni* Kearney) while leaving the southern taxon nameless. Here we rectify that omission.

### MATERIALS AND METHODS

Plants of *C. breweri sensu lato* were collected during 1995–1997, sampling both the northern and southern forms (Table 1). Collection sites in Alpine, Mono, and Tuolumne Counties, California, were chosen because they appeared to be the same populations sampled during an earlier study of chromosome numbers (Nygren 1954). Herbarium specimens prepared as vouchers for these collections were deposited at the Oregon State University herbarium (OSC). We maintained at least 30 individuals from each population (except 20 from Mt. Jefferson) in the Oregon State University Greenhouse. In addition, we examined specimens from the herbaria at California Acad-

emy of Science, Oregon State University, University of California at Berkeley, Humboldt State University, Rancho Santa Ana Botanic Garden, and the Jepson Herbarium. We also borrowed the isotype specimen of *C. breweri* from Harvard University and the type specimen of *C. lemmoni* from the Smithsonian Institution.

Sixteen specimens from 14 northern populations and 23 specimens from at least 17 southern populations were scored for morphological traits. Specimens used for this study are asterisked in the Appendix; all were collected in the wild. The nine morphological characters scored were leaf width (measured near the center of leaves of innovations), panicle length, panicle width, outer glume length, inner glume length, first lemma length, callus beard hair length, awn length, and anther length. Results were analyzed by 2-tailed t-tests, using Statview (Abacus Concepts 1988).

Leaf cross sections were cut by hand from the center portion of mature innovation leaves (those not on culms) from all 16 northern specimens with innovation leaves, plus 19 of the southern specimens. Unstained sections were examined under a compound microscope at 100× and drawn free-hand.

For isozyme analysis, leaf tissue was ground in a tris buffer, pH 7.5 (Soltis et al. 1983), using 1 g polyvinylpyrrolidone-40 per 25 ml. Wicks prepared from Whatman 3 mm chromatography paper were soaked in the resulting slurry and stored at -70°C. Methods of electrophoresis follow the general methodology of Wendel and Weeden (1989). All enzymes were resolved on 12% starch gels. A histidine citrate buffer, pH 5.7 (Soltis et al. 1983) was used to resolve glyc-

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TABLE 1. 1995-1997 COLLECTION SITES FOR ALPINE CALAMAGROSTIS.

Species	Voucher specimen collector, number	Date	State	County	Location	Latitude/Longitude
<i>C. breweri</i>	Sami Gray and Barbara L. Wilson 8269	17 August 1996	California	Alpine	Carson Pass	38.67N 119.99W
<i>C. breweri</i>	Sami Gray and Barbara L. Wilson 8258	16 August 1996	California	Trinity	Mt. Eddy	41.35N 122.54W
<i>C. breweri</i>	Barbara L. Wilson s.n.	11 September 1995	Oregon	Hood River	Mt. Hood	45.34N 121.72W
<i>C. breweri</i>	Mike Roantree s.n.	19 October 1995	Oregon	Marion	Mt. Jefferson	44.70N 121.82W
<i>C. muiriana</i>	Sami Gray and Barbara L. Wilson 8044	30 August 1995	California	Mono	Tioga Pass	37.92N 119.26W
<i>C. muiriana</i>	Sami Gray and Barbara L. Wilson 8901	1 August 1997	California	Tuolumne	Mt. Dana	37.89N 119.26W

eraldehyde-3-phosphate dehydrogenase (G3PDH), malate dehydrogenase (MDH), phosphogluconate dehydrogenase (6PGD), and phosphoglucomutase (PGM). A tris citrate buffer, pH 7.2 (Soltis et al. 1983) was used to resolve isocitrate dehydrogenase (IDH). A lithium borate buffer, pH 8.3 (Soltis et al. 1983) was used to resolve glutamate-oxaloacetate transaminase (GOT), isocitrate dehydrogenase (IDH), and triosephosphate isomerase (TPI). Superoxide dismutase (SOD) resolved as clear bands on gel slices stained for TPI. Enzyme stain recipes followed Wendel and Weeden (1989). For quality control, nearly all specimens were run and stained two to eight times for each buffer/enzyme combination.

Some isozyme samples were prepared from wild-collected leaves, and some from leaves grown by plants held in the greenhouse for as much as three years. When samples were prepared from both wild-collected and greenhouse-grown leaves of the same individual, the isozyme patterns were identical. Therefore, all samples were pooled for analysis.

The southern *Calamagrostis* sampled are assumed to be tetraploid and the northern ones are assumed to be hexaploid, based on Nygren (1954) and the herbarium specimens *Stebbins 5005* and *Stebbins 5006*, which are vouchers for chromosome counts. Both tetraploid and hexaploid individuals exhibit normal meiosis and may reproduce sexually (Nygren 1954). However, because of the complicated banding patterns observed, and because of lack of crossing studies to determine inheritance of bands in these species, we were unable to identify specific alleles and loci for some enzymes. Therefore, a phenotypic instead of genotypic analysis was performed. Results from these eight enzyme stains were treated as nine enzymes, because cystolic and plastid forms of GOT were readily distinguished on gels. Bands and patterns were analyzed in Popgene version 1.21 (Yeh et al. 1997), using haploid settings. Phenotypic diversity measures were calculated from both band presence/absence and multi-band patterns. For presence/absence data, phenotypic diversity was measured by a polymorphic index (P.I.) based on frequency of occurrence of each band.  $P.I. = \text{sum of } f(1 - f)$ , where  $f$  = the frequency of a band in a population (Chung et al. 1991). For multi-band patterns, phenotypic diversity measures included: (1) number of patterns found in each population, (2) percent of stains that yield more than one pattern, (3) average number of patterns per stain in each population, and (4) Shannon-Weaver Diversity Index values (Shannon and Weaver 1949), based on frequency of each pattern in each population. Phenotypic relationships among populations were determined by calculating Hedrick's phenotypic identities (Hedrick 1971) for band data and for multi-band pattern data.

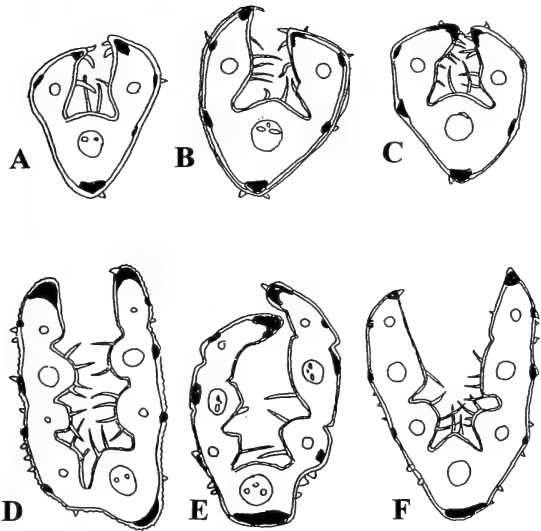


FIG. 1. Leaf cross sections of *Calamagrostis breweri* and *C. muiriana*. A–C. *Calamagrostis muiriana*. D–F. *Calamagrostis breweri*.

RESULTS AND DISCUSSION

Morphology

Foliage characteristics distinguished northern and southern forms. In the southern form, leaves of the innovations (tillers) were involute and extremely thin (0.2–0.35 [–0.4] mm wide) with three (rarely four) veins (Fig. 1A–C). In the northern plants, such leaves were wider ([0.35] 0.4–0.6 mm wide when rolled, 0.9–1.1 mm wide when flat) with seven or more veins (Fig. 1D–F). These foliage differences between the taxa remained conspicuous

over years of greenhouse growth. As reported by Nygren (1954), southern and northern *C. breweri* also differed in morphology of the flag leaf (uppermost leaf on the flowering culm). Northern plants had about ten veins in flag leaves, while southern plants characteristically had five. Differences in leaf size and shape may be attributable to the difference in chromosome number between the northern and southern populations; higher ploidy level is often associated with wider but shorter leaves (Tal 1980).

The two forms also differed in inflorescence characters, with statistically significant differences in panicle length, panicle width (which is, however, strongly influenced by maturity), length of outer glume, and length of longest callus beard hairs (Table 2). Although morphological differences between northern and southern populations were small, they were consistent.

Isozyme Analysis

Isozyme band patterns for the enzymes GOTS, PGD, and TPI readily distinguished southern from northern populations (Table 3). With the exception of Mt. Hood and Mt. Jefferson, all populations were distinguished by MDH patterns (Table 3). All isozyme bands and patterns observed in the invariant Mt. Jefferson population were also observed in Mt. Hood populations, even though the Mt. Jefferson sample included four subpopulations. Little isozyme variation was observed within populations, and two populations (Mt. Jefferson and Mt. Dana) were invariant (Table 4).

Hedrick’s phenotypic similarity based on frequencies of isozyme band patterns (Table 5) was used to estimate similarity of the *Calamagrostis*

TABLE 2. COMPARISON OF CERTAIN MORPHOLOGICAL CHARACTERS IN *C. MUIRIANA* FROM *C. BREWERI*.

Characteristic (units)	Taxon	Sample size	Mean (s.d.)	p =	Range
Leaf width (mm)	<i>C. breweri</i>	15	0.46 ± 0.018	0.0001	0.4–0.6
	<i>C. muiriana</i>	20	0.27 ± 0.012		0.2–0.4
Leaf vein number	<i>C. breweri</i>	14	7.2 ± 0.121	7.4 × 10 <sup>–18</sup>	7–9
	<i>C. muiriana</i>	19	3.1 ± 0.072		3–4
Panicle length (cm)	<i>C. breweri</i>	16	7.0 ± 0.20	0.0001	5.7–8.4
	<i>C. muiriana</i>	22	4.1 ± 0.18		1.9–7.5
Panicle width (cm)	<i>C. breweri</i>	16	2.2 ± 0.32	0.0343	0.7–5.2
	<i>C. muiriana</i>	21	1.4 ± 0.18		0.4–3.0
Length of outer glume (mm)	<i>C. breweri</i>	16	4.05 ± 0.12	0.0005	3.1–4.9
	<i>C. muiriana</i>	23	3.5 ± 0.08		3.0–4.4
Length of inner glume (mm)	<i>C. breweri</i>	16	3.4 ± 0.09	0.0778	3.3–4.5
	<i>C. muiriana</i>	23	3.7 ± 0.08		3.0–4.5
Lemma length (mm)	<i>C. breweri</i>	16	3.3 ± 0.10	0.3338	2.6–4.0
	<i>C. muiriana</i>	23	3.2 ± 0.06		2.6–3.8
Callus beard hair length (mm)	<i>C. breweri</i>	16	0.7 ± 0.06	0.0001	0.3–1.2
	<i>C. muiriana</i>	23	0.4 ± 0.02		0.3–0.6
Lemma awn length (mm)	<i>C. breweri</i>	16	4.6 ± 0.15	0.5693	3.4–5.5
	<i>C. muiriana</i>	23	4.5 ± 0.09		3.3–5.9
Anther length	<i>C. breweri</i>	11	2.0 ± 0.12	0.1782	1.3–2.6
	<i>C. muiriana</i>	18	1.8 ± 0.09		0.9–2.3

TABLE 3. FREQUENCIES OF VARIABLE ISOZYME PATTERNS IN *CALAMAGROSTIS MUIRIANA* (TIOGA AND DANA POPULATIONS) AND *C. BREWERI* (HOOD, JEFF, CARSON, AND EDDY POPULATIONS). In addition, enzymes GOTF, G3PDH, IDH, PGM, and SOD were invariant across all tested populations. Blank means frequency = zero.

Enzyme	Pattern	Tioga	Dana	Hood	Jeff	Carson	Eddy	Band pattern
GOTS	A	0.927	1.000	0.036				001
GOTS	B	0.028		0.964	1.000	1.000	1.000	111
MDH	A	0.971	1.000					00100001010001
MDH	B	0.029						11111001010001
MDH	C						0.167	00100001110101
MDH	D						0.567	00101001110101
MDH	E						0.267	00101001010101
MDH	F					0.028		10110001101010
MDH	G					0.111		01100011101011
MDH	H					0.861		00100001101011
MDH	I			0.500	1.000			00100001110100
MDH	J			0.500				00100001101100
PGD	A	1.000	—					111
PGD	B			1.000	1.000	0.286	0.233	011
PGD	C					0.714	0.767	001
TPI	A	1.000	1.000					011
TPI	B			1.000	1.000	0.967	1.000	001
TPI	C					0.033		111

populations. Material from Mt. Dana resolved poorly and no data was obtained for three enzymes (Table 3). Each similarity between the Mt. Dana population another population is based on only six of the nine enzymes assayed. The two southern populations formed one cluster and the four northern populations formed a second (Fig. 2).

Chromosome Numbers

We relied on previously reported chromosome counts for these grasses, and collected from populations in Mono, Tuolumne, and Alpine Counties, California, that are the same populations or very close to the populations sampled in a study of *Calamagrostis* chromosome counts (Nygren 1954). The thin-leaved southern plants appear to be tetraploid, as indicated by published chromosome counts from Mono, and Tuolumne, Counties (Nygren 1954) and counts for herbarium specimens from Mariposa and Mono Counties (Stebbins 5005

and Stebbins 5006). Only hexaploid plants were found in the one northern population (in Alpine County) for which chromosome counts were published (Nygren 1954).

Ecology

Published accounts and labels from 96 collections of the southern and 26 of the northern populations (see Appendix) indicate that the southern and northern populations differ in habitat and abundance. Nygren (1954) reported that tetraploids grew in high mountains at and above 3000 m elevation, while hexaploids grew at 1800 to 2100 m in the woods. Specimen labels show that the altitudinal range of the southern plant is 2484–3900 m (mean = 3191 ± 33 m; n = 73); that of the northern form is 1700–2600 m (mean = 2158 ± 52 m; n = 21). However, that difference may be less important than it appears; both forms grow near timberline, although the southern one also grows above it.

Labels for southern populations frequently list the habitat as moist or dry meadows. (The distinction may be seasonal; the plants grow in floodplains.) While labels for the northern plants are frequently uninformative, three mention trees or shade (Hitchcock & Martins 5413, Stebbins 5009, Stebbins 7771). Northern plants may grow in full sun or partial shade (personal observation), with one population seen in full shade (Susan Nugent personal communication).

Herbarium labels report the southern plant as “abundant” (Sharsmith 2011), “excellent feed and abundant at and above timberline” (Hatton H-11), “large abundance at high altitudes in the Kern . . . . One of the best forage plants of the higher ranges” (Morrow 5), and the “most abundant grass” (Ferris

TABLE 4. ISOZYME PHENOTYPE STATISTICS FOR *CALAMAGROSTIS BREWERI* AND *C. MUIRIANA*. N = sample size/enzyme. P = percent polymorphic enzymes. A = average number of patterns per enzyme. P.I. = polymorphic index (see methods). S-W = Shannon-Weaver Diversity Index.

Population	N*	P*	A*	P.I.	S-W
Tioga	32	22%	1.222	0.3093	0.0248
Dana	24	0%	1.000	0.0000	0.0000
Hood	21	22%	1.222	0.6283	0.0547
Jeff	18	0%	1.000	0.0000	0.0000
Carson	29	33%	1.444	0.6175	0.0492
Eddy	27	22%	1.333	0.6685	0.0508
<i>C. muiriana</i>	44	22%	1.222	0.1989	0.0199
<i>C. breweri</i>	90	44%	2.111	2.0862	0.2784
Over all	134	44%	2.555	3.0702	0.4600

TABLE 5. HEDRICK'S (1971) PHENOTYPIC SIMILARITY BETWEEN POPULATIONS OF *CALAMAGROSTIS BREWERI* (MT. HOOD, MT. JEFFERSON, CARSON PASS, AND MT. EDDY) AND *C. MUIRIANA* (TIOGA PASS AND MT. DANA).

	Tioga	Dana	Hood	Jeff	Carson	Eddy
Tioga						
Dana	0.86138					
Hood	0.45953	0.37223				
Jeff	0.43944	0.344828	0.83399			
Carson	0.46035	0.355837	0.728548	0.705464		
Eddy	0.46713	0.366033	0.737174	0.713429	0.790985	

9824). Southern plants are community dominants, but northern plants are not (personal observation). In contrast, northern plants have been described as occasional at Mt. Eddy (Whipple 1981) and rare in the Lake Tahoe region (Smith 1984) and in Oregon (Anonymous 1995).

Taxonomic History

*Calamagrostis breweri* was first described by Thurber, who wrote that the leaves were "setaceous involute" (Thurber 1880, p. 281). Later descriptions agreed, calling the leaves "usually involute filiform" (Hitchcock 1912; Abrams 1940; Hitchcock and Chase 1950) or "usually involute" (Munz and Keck 1959), or "flat or inrolled" (Greene 1993). Setaceous involute leaves are characteristic of the southern, not the northern, form (personal observation). Thurber based his description of *C. breweri* upon three specimens: *Brewer 2128* from near the summit of Carson's Pass, *Bolander 6098* from the Tuolumne River, and *Lemmon s.n.* from "California." *Calamagrostis breweri* was effectively lectotypified by the citation of *Brewer 2128* as the type (Hitchcock and Chase 1950). We have examined these specimens. *Brewer 2128* and *Lemmon s.n.* are individuals of the northern populations, with relatively wide leaves that rolled up as they wilted. Only *Bolander 6098* has

truly setaceous involute leaves and represents the southern form.

Kearney (1898) apparently observed the same morphological variation within *C. breweri* that prompted this study. He split the taxon into two species, *C. breweri* as the name was commonly applied, and a new species, *C. lemmoni*, characterized by broader leaves. He stated that *C. lemmoni* was "intermediate between *C. deschampsoides* and *C. breweri*" (Kearney 1898). He cited *Lemmon s.n.* as the type specimen. *Lemmon s.n.* is a broad-leaved northern plant, different from the majority of plants to which the name *C. breweri* has been traditionally applied. However, both *Lemmon s.n.* and *Brewer 2128* are broad-leaved northern plants. The name *C. lemmoni* was appropriately relegated to synonymy with *C. breweri* by Hitchcock (1912). Kearney's attempt to split *C. breweri* left the northern form with two names, and the narrow-leaved southern plant nameless. Doubtless this confusion resulted from the fact that leaves of both *Lemmon s.n.* and *Brewer 2128* had wilted and rolled up tightly before pressing, so that they superficially appear to be setaceous involute.

Nygren (1954) detailed the cytology of *C. breweri* and rediscovered the its morphological variation, but did not treat it taxonomically. He found that plants of two southern populations (near Tioga Pass in Mono County and Mt. Dana in Tuolumne County) were tetraploids ( $2n = 28$ ), and plants from a northern population (near Carson Pass, Alpine county) were hexaploids ( $2n = 42$ ). Nygren also noted that the tetraploid and hexaploid forms could be distinguished by the shape of "the uppermost leaf of the straw [culm]" (Nygren 1954). More recently, Greene (1993) acknowledged the range of morphology, describing *C. breweri* leaves as "flat or involute."

CONCLUSIONS

Kearney (1898) was correct that *Calamagrostis breweri* as traditionally understood includes two entities that differ in morphology and habitat. Perhaps the differences between the two taxa are due to consistent differences in chromosome number; ploidy level in itself can affect the morphological traits and habitat preference like those that differentiate the two forms of *C. breweri* (Tal 1980). Ploidy levels can represent barriers to gene flow,

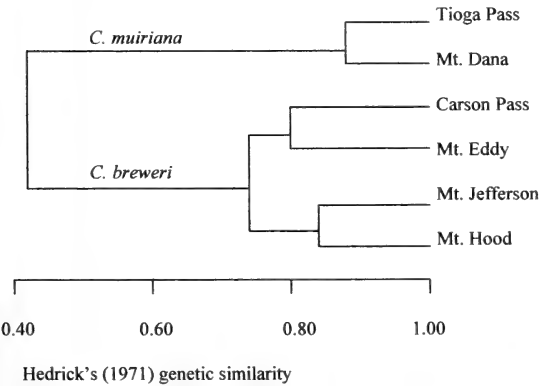


FIG. 2. Cluster diagram based on Hedrick's similarities of *Calamagrostis breweri* (Mt. Hood, Mt. Jefferson, Carson Pass, and Mt. Eddy populations) and *C. muiriana* (Tioga Pass and Mt. Dana populations), calculated from isozyme pattern frequencies.

and therefore populations that differ in chromosome number may be treated as separate species (Harlan and de Wet 1971). However, ploidy level may mean little taxonomically; grasses of two ploidy levels may mingle in a population without obvious morphological or ecological differentiation (Hultquist et al. 1997; Keeler et al. 1987). Taxonomists should avoid encumbering the taxonomic literature with species that differ only in ploidy level (Lewis 1980), but in *C. breweri* the southern (presumably tetraploid) and northern (presumably hexaploid) forms exhibit sufficient morphological, ecological, leaf anatomical, and isozyme differences that they can reasonably be recognized as different species.

We name the southern species after John Muir, pioneering naturalist and first president of the Sierra Club. Muir wrote extensively about the Sierras and in particular the Yosemite area. In the summer of 1869, he spent more than a month in Big Tuolumne Meadows "sketching, botanizing, and climbing among the surrounding mountains" (Muir 1894, p. 70). He must frequently have walked or slept on this small reedgrass that carpets the floodplain meadows of the Yosemite region.

***Calamagrostis muiriana*** B. L. Wilson and Sami Gray sp. nov.—TYPE: USA: California: Tuolumne County: Yosemite National Park; Dana Fork, Tuolumne River, Elevation: 9525 feet. 1 August 1997. *B. L. Wilson and S. Gray 8909*. (Holotype: OSC; isotypes, CAS, NY, RSA, UC, US, UTC).

Gramen pusillum alpinum, maxime simile *Calamagrostidi breweri*, sed tetraploideum et foliis angustioribus trinerviis. Gramen perenne caespitosum, 12–34 cm altum, culmis florentibus folia excedentibus. Folia perangusta glauca, vaginis foliorum marginibus imbricatis, ligulatis 0.8–2.2 mm longis, laminis filiformibus glaucis glabris, 4–12 cm longis, 0.2–0.4 mm latis, venis ternis. Inflorescentia paniculata erecta, pauciflora, atrovioleacea, 1.9–7.5 cm longa, ramis expansis. Spiculae atrovioleaceae, uniflorae, rachilla sterili pilis albis, glumis aequalibus, 3–4.5 mm longis, atrovioleaceis, attenuatis vel minutae aristatis. Lemma hyalinum vel atrovioleaceum, 2.5–4.0 mm longa, apicale denticulatum, dentibus quatuor, pusillis, atrovioleaceis, pilis calli albis 0.3–0.6 mm longis, arista lemmatis geniculata, 3.3–6.0 mm longa, infra medium carinae orienti. Palea hyalina, lemmati aequanti. Antherae maturae 0.9–2.5 mm longae, purpuratae. Species tetraploidea, chromosomata 28.

Gramen abundans in pratis alpinis apricis, distributum in montibus excelsis Californiae centralis.

A *Calamagrostide breweri* laminis angustioribus venis ternis, paniculis pusillioribus, pilis calli brevioribus distinguenda.

Plants caespitose, with intravaginal shoots. Young plants densely tufted. Old plants spreading outward

while dying in the middle and thus forming rings 3 dm or more in width. Foliage glaucous, 6–15 cm long. Leaf sheaths open, glabrous to retrorsely short-pubescent. Ligules 0.8–2.2 mm long, entire, rounded apically. Leaf blades involute, well-developed leaves 4–12 cm long 0.2–4 mm wide as involute, (but earliest leaves of innovations with blades ca. 0.5 cm long and 0.2–0.4 mm wide), leaf blades abaxially scabrous on veins and glabrous or scabrous between them, adaxially pubescent; leaf blades of innovations with 3 (–5) veins and usually 7 sclerenchyma bundles; leaf blades of culms with 5 veins. Leaf tip straight-sided, not prow-shaped. Flowering culms taller than the foliage and 12–35 cm tall. Inflorescence a spreading panicle, few-flowered, 1.9–7.5 cm long and 0.4–3.0 cm wide, dark purple or rarely straw-colored. Spikelets one-flowered, with a sterile rachilla about half as long as the floret and covered with long white hairs. Glumes equal in length, 3–4.5 mm long, thin-textured, purple, often with hyaline margins distally (occasionally straw-colored), acute to apiculate, minutely awned, or attenuate, rounded on the back or keeled distally, glabrous (occasionally scabrous), sometimes with hairs on the keel. Lemma 2.5–4.0 mm long, thin-textured, hyaline or dark purple, glabrous or scabrous, usually with purple on veins distally, the veins extending as four short (ca. 0.5 mm long) teeth. Callus beard hairs white, 0.3–0.6 mm long. Lemma awn purple, arising from below the middle of the lemma, 3.3–6.0 mm long, geniculate, extending beyond the glumes. Palea hyaline, pigmented along veins distally, about as long as the lemma. Mature anthers 0.9–2.5 mm long, purple.  $2n = 28$ .

Descriptions of *Calamagrostis breweri* are, in most instances, descriptions of *Calamagrostis muiriana*. We therefore re-describe *Calamagrostis breweri sensu stricto* here:

Plants caespitose, with intravaginal (occasionally extravaginal) shoots. Young plants densely tufted. Old plants spreading outward while dying in the middle and thus forming rings ca. 1.5 dm in diameter. Foliage glaucous, 10–20 cm long. Leaf sheaths open, scabrous. Ligules 1.7–4.1 mm long, entire to erose. Leaf blades flat but readily rolling when dry, well-developed leaves (2–) 10–15 cm long, 0.4–0.6 mm wide when rolled, the innovation leaves 0.9–1.1 mm wide when flat, (earliest leaves of innovations only slightly reduced), the culm leaves 1.3–1.7 mm wide when flat, leaf blades abaxially scabrous, adaxially pubescent; leaf blades of innovations with 7–9 veins and 9–11 abaxial sclerenchyma bundles; leaf blades of culms often with 11 or more veins. Leaf tip prow-shaped. Flowering culms taller than the foliage and 29–54 cm tall. Inflorescence a spreading panicle, few-flowered, 5.7–8.4 cm long, and 0.7 to 5.2 cm wide, pale to dark purple. Spikelets one-flowered, with a ster-



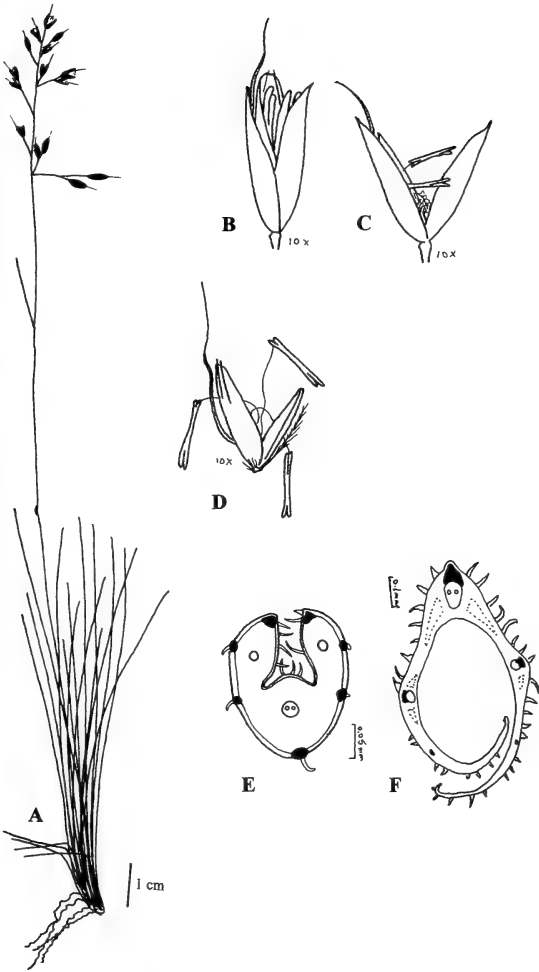


FIG. 3. *Calamagrostis muiriana*. A. habit. B & C. spikelets. D. floret. E. cross section of leaf blade. F. cross section of leaf sheath.

ile rachilla about half as long as the floret and covered with long white hairs. Glumes subequal in length, the lower 3.1–4.9 mm long; the upper 3.3–4.5 mm long. Glumes thin-textured, pale to dark purple or sometimes greenish, often with hyaline margins distally (occasionally straw-colored), acute to apiculate, minutely awned, or attenuate, rounded on the back or keeled distally, glabrous (occasionally scabrous), sometimes with hairs on the keel. Lemma 2.6–4.0 mm long, thin-textured, hyaline or dark purple, glabrous or scabrous, usually with purple on veins distally, the veins extending as four short teeth. Callus beard hairs white, 0.3–1.2 mm long. Lemma awn purple, arising from below the middle of the lemma, 3.4–5.5 mm long, geniculate, extending beyond the glumes. Palea hyaline, pigmented along veins distally, about as long as the lemma. Mature anthers 1.3–2.6 mm long, purple.  $2n = 42$ .

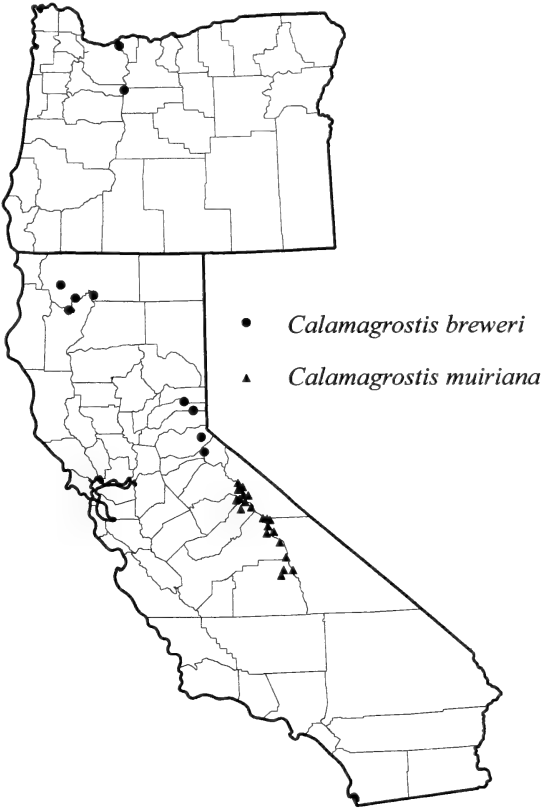


FIG. 4. Distribution of *Calamagrostis breweri* (●) and *C. muiriana* (▲) in Oregon and California.

KEY TO ALPINE REEDGRASSES OF WESTERN NORTH AMERICA

1. Leaves extremely thin and involute, 0.25–0.4 mm wide as rolled, with 3 (–4) veins, the tip straight-sided; panicle length 1.9–5.7 cm; callus beard hair length 0.3–0.6 mm; range south of Sonora Pass (Yosemite area and south; Fig. 4) . . . . . *C. muiriana*
1. Leaves narrow, flat in life but readily rolling when wilted, 0.4–0.6 mm wide as rolled, with 7 or more veins, the tip prow-shaped; panicle length 5.7–8.5 cm; callus beard hair length 0.3–1.2 mm; range north of the Sonora Pass (Carson Pass area north to Mt. Hood, Oregon) . . . . . *C. breweri* s. str.

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## APPENDIX 1

## SPECIMENS EXAMINED

\* = specimen included in morphometric study;

\*\* = type specimen

*Calamagrostis muiriana*: USA: **California**: **Fresno Co.**, Baxter Lake, 6 Sep 1959, *DeDecker 1119* (CAS); N of Kings River, Red Mt. Basin, 16 Aug 1961, *Hardham 8748* (CAS); Silver Pass in Fish Creek Country; Sierra Nat'l Forest; 19 Sep 1912, *Hatton H-109* (CAS); Death Pond, Kaiser Ridge, 12 Aug 1928, *Jepson 13229\** (UC); Bear Cr. Watershed, Mt. Hilgard, 20 Aug 1951, *Quibell 680* (RSA); Bear Cr. Watershed, 2 mi W of Mt. Hilgard, 21 Aug 1951, *Quibell 767* (RSA); Bighorn Lake, headwaters N Fk Mono Cr., 2 mi W of Red & White Mt., 31 Aug 1952, *Quibell 1575* (RSA); Bighorn Lake, headwaters N Fk Mono Cr., 2 mi W of Red & White Mt., 31 Aug 1952, *Quibell 1583* (CAS); Bear Creek, near Florence Lake, 7 Sep 1954, *Quibell 4985* (OSC, RSA); Upper French Canyon Basin (near Bishop), 6 Aug 1955, *Quibell 5387* (RSA); Colby Meadows, 24 Jul 1952, *Raven 4677* (CAS); Laurel Creek, 13 August 1953, *Raven 6174* (CAS); Rose Lake, 8 Aug 1954, *Raven 7858* (CAS); Bench Lake, 25 Jul 1956, *Raven 9846* (CAS); Humphrey's Basin, W of Mt. Humphreys, 12 Aug 1937, *Sharsmith 3165\** (CAS, UC); Mono Pass, 118°50'W, 37°25'N, 10 Sep 1959, *Thomas 8144* (CAS); Second Recess, 18 Jul 1953, *Raven 5694* (CAS); **Inyo Co.**, Paiute Pass; 11,300–11,409 ft., 22 Jul 1934, *Ferris 8877\** (CAS, UC); Rock Cr. Lake Basin, Mosquito Flat, 14 Jul 1946, *Howell 22277* (CAS); Mono Mesa, 26 Jul 1946, *Howell 22730* (CAS); Big Pine Lakes, 5th Lake, 5 Aug 1947, *Howell 23767* (CAS, RSA); Rock Cr. Lake Basin (Long Lake), 22 Jul 1931, *Peirson 9398* (RSA); Rock Cr. Lake Basin, 17 Jul 1931, *Peirson 9399* (RSA); Rock Cr. Lake Basin, Ruby Falls, 20 Jul 1934, *Peirson 12617\** (CAS, RSA, UC); Coyote Ridge, 7 Aug 1950, *Raven & Stebbins 217* (CAS); Coyote Ridge, 2 Aug 1950, *Raven & Stebbins 227\** (UC); Mono Pass; Ruby Lake, 16 Jul 1936, *Robinson 689* (RSA); Lone Pine Canyon, E of Mt. Muir, 20 Aug 1937, *Sharsmith 3310\** (UC); Mono Mesa near junction of Mono, Inyo, & Fresno Co., 37°28'N, 118°46'W, 9 Sep 1961, *Thomas 9747* (CAS); **Madera Co.**, Lyell Fork of Merced River, Yosemite Nat'l Park, 1 Aug 1931, *Blasdale s.n.* (UC); Minarets, 23 Aug 1918, *Grant 1585* (CAS); Minarets, 23 Aug 1918, *Grant 1587* (CAS); **Mariposa Co.**, Soda Springs by the Tuolumne, 15 Aug 1894, *Congdon s.n.* (CAS); Yosemite Nat'l Park, ½ mi N of Tenaya Lake, 18 Jul 1951, *Stebbins 5005\** (UC); Emeric Lake, T2S R24E S8, 15 Sep 1935, *Thomas 490\** (UC); May Lake, 15 Jul 1977, *Vale s.n.* (CAS); **Mono Co.**, Slate Cr. Basin, E of Mt. Conness, 7 Sep 1934, *Clausen 922* (CAS); Tioga Pass, Yosemite Nat'l Park boundary, 16 Aug 1936, *Ferris 9824\** (CAS, UC); Tioga Pass, just S of entrance to Yosemite Nat'l Park, *Heller 15461* (CAS); Mono Pass, 16 Aug 1944, *Howell 20631* (CAS); Saddlebag Lake,

head of Lee Vining Cr., 18 Jul 1968, *Howell & True 4432* (CAS); Saddlebag Lake, head of Lee Vining Cr., 18 Jul 1968, *Howell & True 4435* (CAS); Slate Cr. Basin, 26 Aug 1937, *Keck 4591* (CAS, UC); HM Hall Natural Area, Green Lake, N base of Mt. Conness, 27 Aug 1927, *Keck 4610* (CAS); HM Hall Natural Area; saddle between Mt. Conness & East Plateau, 27 Aug 1927, *Keck 4631* (CAS); Slate Cr. Valley, Inyo Nat'l Forest, 26 Jul 1954, *Krueberg 3602* (CAS, RSA); Slate Cr., 17 Aug 1954, *Munz 19987* (RSA); Slate Cr., Aug 1954, *Munz 20088* (RSA); Saddlebag Lake, 18 Jul 1968, *Rose 68151* (CAS, HSC, RSA); Tioga Pass, 14 Aug 1930, *Stanford 2029* (RSA); summit of Dana Plateau; 10 km W of Mono Lake, 19 Jul 1951, *Stebbins 5006\** (UC); Mono Basin, Parker Cr. Basin, 1 Aug 1987, *Taylor 9210\** (RSA, UC); Mono Pass, 4th Recess, 37°26'N, 118°48'W, 11,000–12,000 ft., 13 Sep 1954, *Thomas & Thomas 4630* (CAS); Mt. Conness Region, NE of Steelhead Lake, 11 Sep 1959, *Twisselmann 5700* (CAS); Saddlebag Lake, 16 Aug 1933, *Wolf 5334* (RSA); below Highway 120 near Yosemite E entrance, 11 Aug 1970, *Wood 242* (HSC); near Tioga Pass, T1N R25E S30, 22 Aug 1936, *Yates 6301* (RSA, UC); Tioga Pass, T1N R25E S30, 22 Aug 1936, *Yates 6304\** (CAS, UC); a mile above Conness Lake, Convict Cr. drainage, 26 Aug 1968, *Zufeldt 2* (CAS); **Tulare Co.**, Kern Lake, 11,000–12,100 ft. CAP 2074\* (UC); Mt. Whitney, 11 Jul 1910, *Clemens s.n.* (CAS); Yosemite Nat'l Park, Mt. Conness, 19 August 1897, *Dudley 1703* (CAS); between Reflection Lake & Harrison Pass, 8 Aug 1940, *Howell 16048* (CAS); Little Five Lakes Basin, 29 Jul 1942, *Howell 17379* (CAS); Sky Parlor Meadow, Chagoopa Plateau, 1 Aug 1942, *Howell 17520* (CAS); Center Basin, 26 Jul 1948, *Howell 25042* (CAS, RSA); Rock Creek, 21 Jul 1949, *Howell 25568\** (CAS, UC); Mineral King vicinity, Farewell Gap, 20 Jul 1951, *Howell 28013* (CAS, RSA); Mineral King Vicinity, White Sheif Region, 21 July 1951, *Howell 28088* (CAS); Diamond Mesa, 25 Jul 1954, *Kehrlein* (CAS); Kern Nat'l Forest (Mt. Whitney District), *Morrow 5* (CAS); Mineral King Game Refuge, Sequoia Nat'l Forest, N of Franklin Lakes, 8 Aug 1966, *Rice 516* (OSC, RSA); Kern Plateau, *Twisselmann et al. 11280* (RSA); Chicken Spring Lake, Kern Plateau, 31 Jul 1970, *Twisselmann et al. 17396* (CAS, RSA); **Tuolumne Co.**, Tuolumne Meadows, September 1866, (*Bolander?*) 6098\* (UC); Tuolumne Meadows, Yosemite Nat'l Park, *Babcock 3627* (UC); Slide Canyon W of Finger Peak near N boundary of Yosemite Nat'l Park, 31 July 1934, *Bartholomew s.n.* (UC); Mt. Lyell Quadrangle, 2 miles W of Mt. Gibbs, 6 Aug 1937, *Bufford s.n.\** (UC); Yosemite Nat'l Park, Lake Ireland, 29 Jul 1917, *Clemens s.n.* (CAS); Mt. Dana, 16 Aug 1894, *Congdon s.n.\** (CAS, UC); Yosemite Nat'l Park, Mt. Conness, 9 Aug 1934, *DeRoy 115* (CAS); Gaylor Lake (upper), Yosemite Nat'l Park, *Hall 11864* (CAS, UC); Tioga Pass, Yosemite Nat'l Park, 13 Sep 1922, *Hall s.n.* (CAS); Dog Lake, 6 Aug 1944, *Howell 20034* (CAS); Gaylor Lake, 12 Aug 1944, *Howell 20372\** (CAS, UC); Lyell Fk of Tuolumne River, 25 Jul 1936, *Lee 2334\** (UC); Yosemite Nat'l Park, 12 Mar 1909, *Lemmon 1897* (CAS); Tioga Pass, 30 Aug 1957, *Rose 57127* (CAS, RSA, UC); Lyell Fk. of Tuolumne River, upper Lyell Can-

yon, 25 Jul 1933, *Sharsmith 189* (CAS, UC); Dana Meadows, west base of Mt. Dana, 15 Aug 1933, *Sharsmith 414\** (UC); Mt. Dana, west slope, 1 Aug 1931, *Sharsmith 800* (UC); Mt. Dana, NW plateau, 10 Sep 1934, *Sharsmith 2100* (CAS, US); Mt. Dana, NW slope, 2 Aug 1933, *Sharsmith 257B* (UC); Gaylor Lake, Yosemite Nat'l Park, 23 June 1976 *Vale & Wagnon s.n.* (CAS); Tuolumne Meadows, Mt. Lyell Quadrangle, 22 Aug 1936, *Yates 6325\** (CAS, RSA, UC); Tuolumne Meadows, Yosemite Nat'l Park, 8500–9500 ft., Jul 1902, *Hall & Babcock 3627* (UC).

*Calamagrostis breweri*: USA: **California: Alpine (?) Co.**, near summit of Carson's Pass, *Brewer 2128\*\** (GH, US); Lake Winnemucca ca. 2 miles south of Carson Pass, 17 Aug 1996, *Gray & Wilson 8270* (OSC); **Amador Co.**, Woods Lake, summit of Carson Pass, 20 Jul 1951, *Stebbins 5009\** (UC); **Eldorado Co.**, Echo Lake, 11 Aug 1981, *Best s.n.\** (CAS); E side Wright's Lake, T12N R16E, 16 Jul 1977, *Stebbins 7771\** (CAS); Trail from Suzie to Heather Lake, 17 Aug 1928, *Wolf 3338\** (RSA); **Nevada Co.**, Basin Peak, 27 Aug 1968, *True 4590\** (CAS); 1 mi SW of Mt. Lola, White Rock Lake, 7920–8400 ft., 28 Jul 1976, *Trowbridge 8000\** (CAS); 1 mi SW of Mt. Lola, White Rock Lake, 28 Jul 1976, *Trowbridge 8074* (CAS); **Placer Co.**, Donner Pass, 10 Aug 1903, *Heller 7130\** (CAS, OSC, UC); **Siskiyou Co.**, English Peak, Diamond Lake, 2 Aug 1968, *Oettinger 345\** (RSA); English Peak, Marble Mt. Wilderness Area, Shasta Ridge, 3 Sep 1969, *Oettinger 1613\** (RSA, UC); Shasta Ridge, N slope of English Peak, 3 Sep 1969, *Oettinger 1613* (HSC); S side Caribou Lake, T37N R10W S35, 19 Aug 1980, *Renner 2506* (HSC); above Sugar Lake, T40N R9W S31, 4 Aug 1969, *Sawyer 1803\** (OSC); above Sugar Lake, 4 Aug 1969, *Sawyer 1803* (HSC); W of Little Duck Lake, T40N R9W S19, 14 Sep 1972, *Smith & Sawyer 5813* (HSC); Mt. Eddy, north face, T40N R5W S7, 25 Jul 1976, *Whipple 1576* (HSC); Mt. Eddy, north slopes, T40N R5W S7, 20 Jul 1977, *Whipple 2006* (HSC); near Little Crater Lake, T40N R5W S5&6, 5 Aug 1977, *Whipple 2183* (HSC); 1.45 mile by road north of Parks Creek Summit, T41N R6W S33, 16 Aug 1996, *Wilson & Gray 8258* (OSC); **Trinity Co.**, Stuart Fk. drainage, west of Morris Lake, T36N R10W S22, 24 Aug 1997, *Ferlatte 1899\** (HSC, UC); Lower Canyon Cr. Lake, 10 mi W of Dedrick, Salmon-Trinity Alps, 11 Jul 1939, *Hitchcock & Martins 5413\** (CAS, UC); Echo Lake, T35N R9W S3, 12 Aug 1994, *Rolle 853* (OSC); **California, no county**, [no location], *Lemmon s.n.\*\** (US); [no location], 18 Feb 1909, *Lemmon s.n.* (US); **Oregon: Hood River Co.**, Mt. Hood (SE; upper Sahalie Falls), 2 Aug 1924, *Henderson 1045 of 1924\** (CAS, OSC); Mount Hood Meadows Ski Area, T3S R9E S4, 11 Sep 1995, *Laub s.n.* (OSC); Mt. Hood, Heather Canyon, T2S R9E S24, 1 Aug 1999, *Nugent s.n.* (OSC); Mt. Hood, T2S R9E S34, *Poff s.n.* (OSC); Mt. Hood, T2S R8.5E S13, 4 Sep 1979, *Siddall s.n.\** (OSC); Paradise Park, Mt. Hood, 11 August 1926, *Thompson 1660*, **Linn Co.**, Jefferson Park, 16 Aug 1946, *Prescott s.n.*, **Marion Co.**, Mt. Jefferson, T10S R5E S11, 9 Sep 1992, *Roantree, s.n.\** (OSC); Mt. Jefferson Wilderness Area, SE end of Russel Lake, T10S R8E S11, 18 Oct 1995, *Roantree, s.n.* (OSC).

PLANT ZONATION IN A SHASTA COUNTY SALT SPRING SUPPORTING  
THE ONLY KNOWN POPULATION OF *PUCCINELLIA HOWELLII*  
(POACEAE)

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ABSTRACT

Three small salt springs adjacent to state highway 299 west of Redding, California, support the only known population of the grass, *Puccinellia howellii* J.I. Davis. The common halophyte grass, *Distichlis spicata* (L.) E. Greene, and *Puccinellia* each dominate different areas within the springs. In 1991, a highway realignment encroached on the *Puccinellia*, and in partial mitigation, an attempt was made to convert a *Distichlis*-occupied area to *Puccinellia*. The subsequent re-occupation by *Distichlis* forced a reconsideration of the restoration rationale and methods, and raised concern for the potential of *Distichlis* to replace *Puccinellia* elsewhere. But a TWINSPLAN of systematically chosen samples suggested that the two grasses are members of distinct vegetation types associated with different hydrology. Salinity and growth monitoring of stands of *Puccinellia* and *Distichlis* suggested that the former tends to occupy areas continually irrigated by spring discharge, while the latter tends to occupy areas that are less directly irrigated, where salt can accumulate during the warm months, but also where precipitation during the cool months can lower the salinity enough to temporarily permit the growth of glycophytic annuals. *Triglochin maritima* L. and *Juncus bufonius* L. were also monitored. Greenhouse tests showed that *Puccinellia* is adversely affected by the high salinity typical of the *Distichlis* areas during summer. The association of *P. howellii* with continual surface flow should be considered when selecting and preparing revegetation sites, and when surveying for new populations.

Key words: *Puccinellia howellii*, salt spring, salt marsh, *Distichlis spicata*, vegetation zonation, halophyte, endemic

Adjacent to State Route 299, approximately 32 km west of Redding, California, near the juncture with Crystal Creek Road, and within the boundaries of the Whiskeytown Recreational Area, are three mineral springs totaling 0.49 hectares (Fig. 1). The low grass cover and the bare and rocky areas contrast sharply with the adjacent canyon live oak and blue oak woodland. The springs discharge from numerous points, producing a sheet flow over much of the site as the water moves downhill. Salinity ranges from 15–35 dS/m (mmho/cm), approximately half that of sea water, with a calcium content of 1–1.8 g/liter. Discharge volume and chemistry remain stable year round (CH2M HILL 1991–1992). Though initially alkaline (pH 9–9.6) the water acidifies (pH 7–5) as it flows away from the discharge points (Fulgham et al. 1997), presumably due to the influence of decomposing organic matter. Typical for this region, precipitation is restricted to a period from mid-fall to mid-spring.

Two halophytic perennial grass species dominate

the site, usually in separate stands, *Puccinellia howellii* J.I. Davis, “Howell’s alkali grass,” a cool season species endemic to this site, and *Distichlis spicata* (L.) E. Greene (including *D. stricta* (Torr.) Rydb.), “salt grass,” a warm season species widespread in both coastal and inland settings in North America.

*Puccinellia howellii* was first recognized as a distinct species in 1990 (Davis). The closest species morphologically is *P. pumila* (Vasey) A. Hitchc., found in coastal marshes from Washington to Alaska, rarely south to California (Kartesz 1999). Although commonly referred to as “alkali grass,” most *Puccinellia* are associated with saline habitat of neutral pH. Although *Puccinellia howellii* is included on the California Native Plant Society List 1B (“rare, threatened or endangered in California and elsewhere”), it currently has no state or federal legal status (CNPS 2001).

*Puccinellia howellii* stands range from sparse to dense, and consist either of individual tufts or a

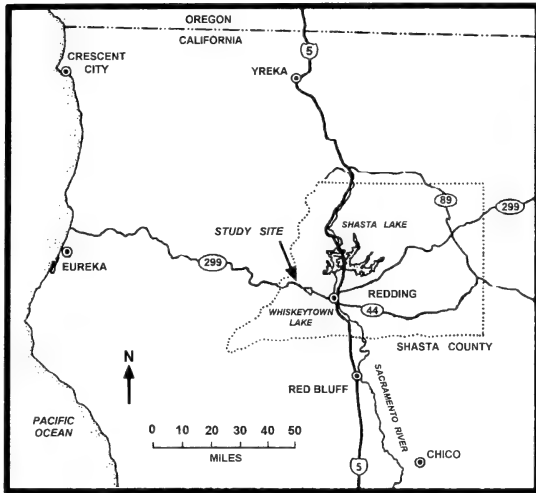


FIG. 1. Location of the study area west of Redding, Shasta County (Bacca 1995).

dense, turf-like growth. Plants at maturity can range in stature from 2.5 to 20 cm or taller, excluding the length of the inflorescences. The tuft form reaches the greatest height. The structure of the tufts suggests that individuals rarely persist longer than several years under field conditions. *Triglochin maritima* L. often co-occurs with *Puccinellia* in the wetter locations.

While *Puccinellia* tends to occupy the central portions of the springs, *Distichlis* is often found at the periphery, adjacent to the surrounding non-saline vegetation. In winter and spring, when *Distichlis* is dormant, the areas occupied by *Distichlis* often support a sparse to dense cover of the annual grass species found outside the springs. At this location, *Distichlis* appears to spread primarily via rhizomes and stolons; little seed production has been observed. In contrast, *Puccinellia* reproduces primarily from seed.

*Juncus bufonius* L., a glycophytic (non-halophytic) annual, seasonally occupies some otherwise barren areas within the springs. The exotic and potentially invasive *Atriplex rosea* L. is present, but was uncommon during the data collection portion of this study.

In 1991, a realignment of State Route 299 encroached on the salt springs. The California Department of Transportation (CalTrans) salvaged *Puccinellia* tufts from the construction zone and transplanted them to an adjacent 176 m<sup>2</sup> area reclaimed from a deposit of roadside spoil occupied by *Distichlis*. An aerial photo predating the spoil suggested that the area had previously been occupied by *Puccinellia*. The site was prepared by removing approximately 1/3 m of soil, which was found to be dense with *Distichlis* rhizomes. After transplanting, the *Puccinellia* tufts quickly became established, and at first produced considerable re-

cruitment from seed. However, by the second year, *Distichlis* rhizomes and stolons began to re-enter from the periphery. By the third year, *Puccinellia* tufts were dying and not being replaced by seedlings, and by 1998, *Distichlis* had replaced *Puccinellia* in most of the transplant area. This unanticipated outcome raised questions about the potential for *Distichlis* to replace *Puccinellia* elsewhere.

Concurrent with the transplant project, CalTrans funded an ecological study of *P. howellii*, which was conducted by the authors between 1993–1995. Drawn from that study (Fulgham et al. 1997), this paper describes plant zonation within the springs, and provides information about the relative habitat requirements of the component species.

## METHODS

**Sampling.** In May 1993, the visible extent of the three springs was systematically surveyed for vegetation analysis. Parallel transects were laid out 3.05 m apart. Along each transect, an initial sampling position was selected randomly, and subsequent positions spaced at 3.05 m intervals. Species percent cover was estimated using a tripod-mounted optical point-intercept bar (Cover-Point/ESCO) with 20 sighting positions along its 1 m length. At each sampling position, the bar was placed perpendicular to the transect, randomly either left or right. Each bar setting constituted a sample. The combination of systematic and randomized elements in the sampling design ensured a uniform coverage, while providing a considerable degree of independence between samples. Because the *Distichlis* growth for the current year had not yet appeared, it was surveyed by using the dead growth from the previous year, which at the time was still structurally intact.

In addition to the collection of species data, the surface moisture at each intercept point was recorded in one of four categories, depending on whether it appeared dry, moist, saturated (i.e., “glistening”), or with standing water.

**Vegetation analysis, association.** The cover samples were analyzed with TWINSpan (Hill et al. 1988). Of the 551 samples, only the 394 with  $\geq 5\%$  cover were used. Pseudospecies cut levels were set at 5, 15, 33, and 67, and each given equal weight. Cover from species found in five or fewer samples were combined into a category “misc”.

**Vegetation analysis, moisture.** A subset of 235 vegetation samples was used to compare the surface moisture associated with each species. As defined, these were plots with  $\geq 15\%$  total cover, and where one species contributed  $>50\%$ . In reality, the large majority of the samples that met these criteria had one species exceeding 66%. To compare the relative moisture between samples, the percent covers for the moisture categories were weighted and summed to form a quasi-continuous moisture index. “Dry” cover was weighted by 0.25, “moist”

TABLE 1. TWINSPAN VEGETATION GROUPS, MEAN COVER AND CONSTANCY. Survey area with 551 samples. Analysis limited to 394 samples with  $\geq 5\%$  cover. Tabulation includes species with constancy  $\geq 5\%$ . n = number of samples. Cov = % cover within the group. Con = % constancy. <sup>1</sup> Pooled from species "misc" (species found in  $\leq 5$  samples), and "PLspp" (*Plantago* spp.). <sup>2</sup> Pooled from *Bromus diandrus*, *B. hordaceus*, *B. rubens*, *Lolium multiflorum*, and *HOspp* (*Hordeum* spp.). <sup>3</sup> All cover, including species with  $< 5\%$  constancy.

	All samples n = 551	TRMA n = 33		PUHO n = 194		SCBO/misc n = 19		DISP/glyco n = 61		DISP/halo n = 43		JUBU n = 44	
	Cov	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con	Cov	Con
<i>Triglochin maritima</i>	1.0	14	100	1	7								
<i>Puccinellia howellii</i>	10.8	1	12	28	100					6	32	1	23
Low frequency glycyophytes <sup>1</sup>	0.8					13	95	2	15				
<i>Scribneria bolanderi</i>	0.6					8	37						
Annual grasses <sup>2</sup>	1.3					1	5	10	63	2	11		
<i>Distichlis spicata</i>	8.6					2	26	54	97	29	98	1	16
<i>Polypogon monspeliensis</i>	0.7					2	11			6	41	<1	7
<i>Juncus bufonius</i>	1.4					1	21			2	20	15	100
Total cover <sup>3</sup>	25.2	15		30		26		66		46		18	

by 0.5, "saturated" by 0.75, and "standing water" by 1.0. The resulting composite values ranged from 25 to 100. A Mann-Whitney test (Minitab 1991) was used to compare the moisture index values of the *Puccinellia* and *Distichlis* samples.

*Species monitoring.* Following vegetation analysis, groups of four 1 × 2 meter plots were assigned to monitor the biotic and edaphic conditions of each of ten vegetation categories of interest, during the period from June 1993 to December 1994. To attempt to identify the conditions responsible for the variability of the *Puccinellia* stands, plots were assigned to monitor six stature and density combinations found within the population. The remaining sixteen plots were assigned to monitor nearly pure stands of the three next largest contributors to cover, *Distichlis*, *Triglochin*, *Juncus bufonius*, and also to barren locations. Initially the plots were randomly assigned to suitable locations identified by the systematic sampling; however, this produced a poor spatial distribution within and between the springs, therefore some plots were reassigned to other random or nearby locations.

Soil samples were analyzed for texture and rock fragment content, and for soluble and exchangeable cations, nitrogen, phosphorus, and organic matter. Soil moisture, salinity, pH, growth and cover were monitored approximately monthly during the period. In the case of *Puccinellia*, additional biotic responses were monitored, such as culm and seed production and seedling survival. This paper reports only salinity and cover. Except for salinity, and to a lesser extent, soil moisture, little difference was noted between the conditions associated with the monitored groups. (Among the *Puccinellia* groups, stature was inversely proportional to rock fragments.) The plots from the high density/medium stature "H3" group will be used to represent *Puccinellia*, because this group seemed to reflect conditions favorable for growth, and the vegetation

in the four plots remained stable for most of the duration of the study.

At each monitoring visit, several soil samples were collected from the periphery of each plot and pooled to form a composite weighing 300–600 g. After air-drying, 100 g portions of the fine-earth fraction were used to determine salinity by the saturated-extract procedure (Roades 1982). The ratio of the water content of the saturated paste to that of the original soil sample was used to convert the electroconductivity to a value presumed equivalent to the original field salinity. For specimens containing precipitated salt at the time of collection, this method produced artificial values exceeding the conductivity of a saturated solution (e.g., 226 dS/M at 25°C for NaCl), but nonetheless roughly proportional to the salt content.

*Greenhouse.* In the greenhouse, *Puccinellia* growth was monitored at five levels of salinity, ranging from 0 to 80 dS/m, using 4 cm *Puccinellia* plants that had been germinated and reared at 20 dS/m, a typical field level. The treatment groups were adjusted to their target level at a rate of 10 dS/m per 8 days. Germination was also monitored under a similar range of salinities.

RESULTS AND DISCUSSION

*Vegetation analysis, association.* According to the point-intercept data, the total vegetative cover was 25.2%, with *Puccinellia* and *Distichlis* 10.8% and 8.6%, respectively. Table 1 lists the cover of the major contributors, and summarizes the mean cover and constancy for the component species of each of the six vegetation groups suggested by TWINSPAN. The dendrogram in Figure 2 shows the sequence of the divisions. TWINSPAN initially segregated two largely monotypic groups from the rest of the data, TRMA (*Triglochin*), and PUHO, the latter capturing 94% of the *Puccinellia* cover.

Level 0

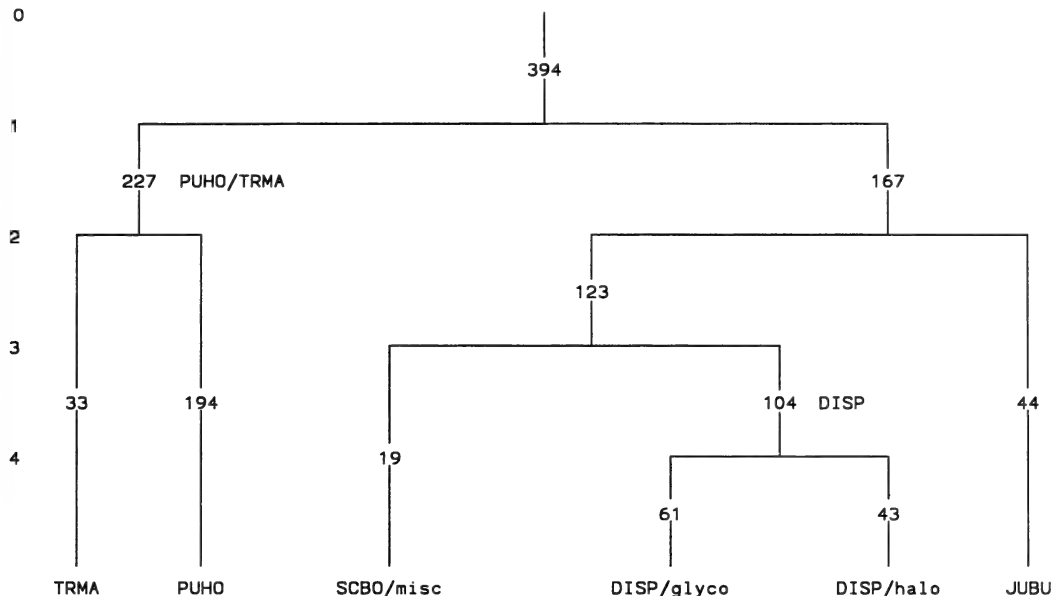


FIG. 2. TWINSpan species dendrogram for 394 vegetation samples. Associations: TRMA = *Triglochin maritima*; PUHO = *Puccinellia howellii*; SCBO/misc = *Scribneria bolanderi*, *Plantago* spp., and miscellaneous low frequency species; DISP/glyco = higher-density *Distichlis spicata* sometimes associated with annual grasses; DISP/halo = lower-density *Distichlis* sometimes associated with *Puccinellia* and *Polypogon*; JUBU = *Juncus bufonius*.

The distinction between TRMA and PUHO, however, was not visually apparent in the field, where the wetter habitat seemed to support both species intermixed. Therefore, it seemed reasonable to regard the two as a single association, PUHO/TRMA.

*Distichlis* was divided between two groups. Approximately two-thirds of the cover was placed in a group that we labeled DISP/glyco, characterized by higher density *Distichlis*, and often accompanied by annual grasses and other glycophytes that are active during the rainy season. *Puccinellia* was notably absent. During the vegetation survey, we regarded the annual grasses as presumably salt-tolerant contaminants, but we revised this view later as we observed *Distichlis* emerge amid the brown stalks of annual grasses in areas beyond the assumed boundary of the salt spring. In the downslope portions of these peripheral and sometimes disjunct zones there were seepages that had not been visible. The accumulating mineral stains and evaporate indicated that during summer, after the cessation of precipitation, salt water was able to reach the surface. We inferred that in the central spring area, the presence of glycophyte grasses amid the *Distichlis* might also indicate a salinity regime that alternates between fresh in winter and saline in summer.

The remaining 1/3 of the *Distichlis*, labeled DISP/halo, had a lower mean density and a smaller glycophytic component. *Puccinellia* and/or *Polypogon monspeliensis* (L.) Desf. were sometimes present. Although the latter is not usually regarded as a hal-

ophyte, it will germinate simultaneously with *Puccinellia* when seed of both species are irrigated directly by salt spring surface flow (Levine personal observation).

The primarily monotypic JUBU, capturing most of the *Juncus bufonius*, also had a small *Puccinellia* component. The heterogeneous SCBO/misc., including nearly all the *Scribneria bolanderi* (Thurber) Hackel and most of the miscellaneous low-frequency glycophytes, consisted of the remaining samples.

**Vegetation analysis, moisture.** The vegetation sampling was performed well after the cessation of seasonal precipitation, when the surface moisture primarily reflected the influence of the spring discharge, but before the evaporative effects of summer heat. Among the 235 samples predominated by a single species, the wetter samples were commonly dominated by *Puccinellia* or *Triglochin*, the drier by *Juncus* and *Scribneria*, and *Distichlis* was intermediate (Fig. 3). A Mann-Whitney test showed that the *Puccinellia* samples had significantly greater surface moisture values than the *Distichlis* ( $P < 0.0001$ ).

**Species monitoring.** Possible insights into the relationship between growth and the salinity regime may be provided by examining the data from the monitoring plots for the four species (Fig. 4a-h). Although the sample size is small, the data suggest that areas occupied by different species may also

samples with one species predominant  
surface moisture histograms

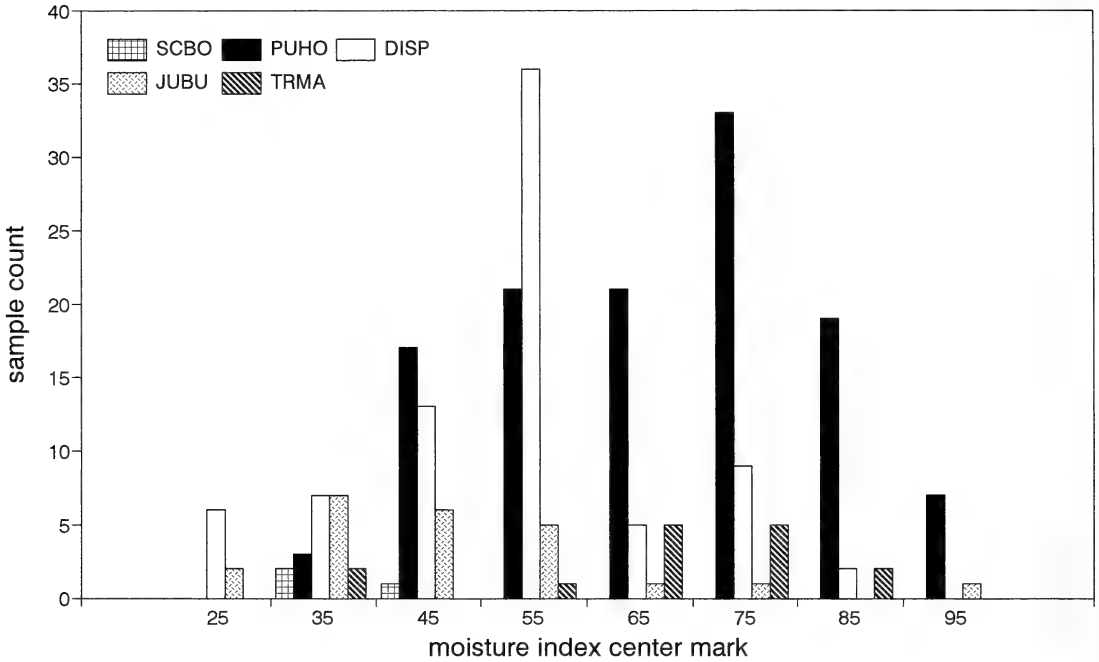


FIG. 3. Histogram of surface moisture for the 235 vegetation samples  $\geq 15\%$  cover, where one species contributed more than 50% (the large majority contributing  $>66\%$ ). The dominant species are indicated by the acronyms defined in Figure 2. Values range from 25 = "dry" to 100 = "standing water".

differ in the annual pattern of salinity, and by inference, the amount of irrigation.

In the *Puccinellia* and *Triglochin* plots (Fig. 4a, c), saline conditions occurred year-round, and rose only moderately during the summer. Apparently, the volume of irrigation was sufficient to minimize the seasonal influence of precipitation or evaporation. In contrast, salinity in the *Juncus* plots and most of the *Distichlis* plots (Fig. 4e, g) was low from fall to spring, and became high during the summer. The exception was *Distichlis* plot #3, which remained saline through the winter. This plot was selected for monitoring because of the atypically short stature and low density, and the adjacency of robust *Puccinellia*, perhaps suggestive of the TWINSPAN group, DISP/halo.

The growth cycles of the four species appear to track the change in salinity. *Puccinellia* (Fig. 4b) has a phenology similar to the glycophytic grasses

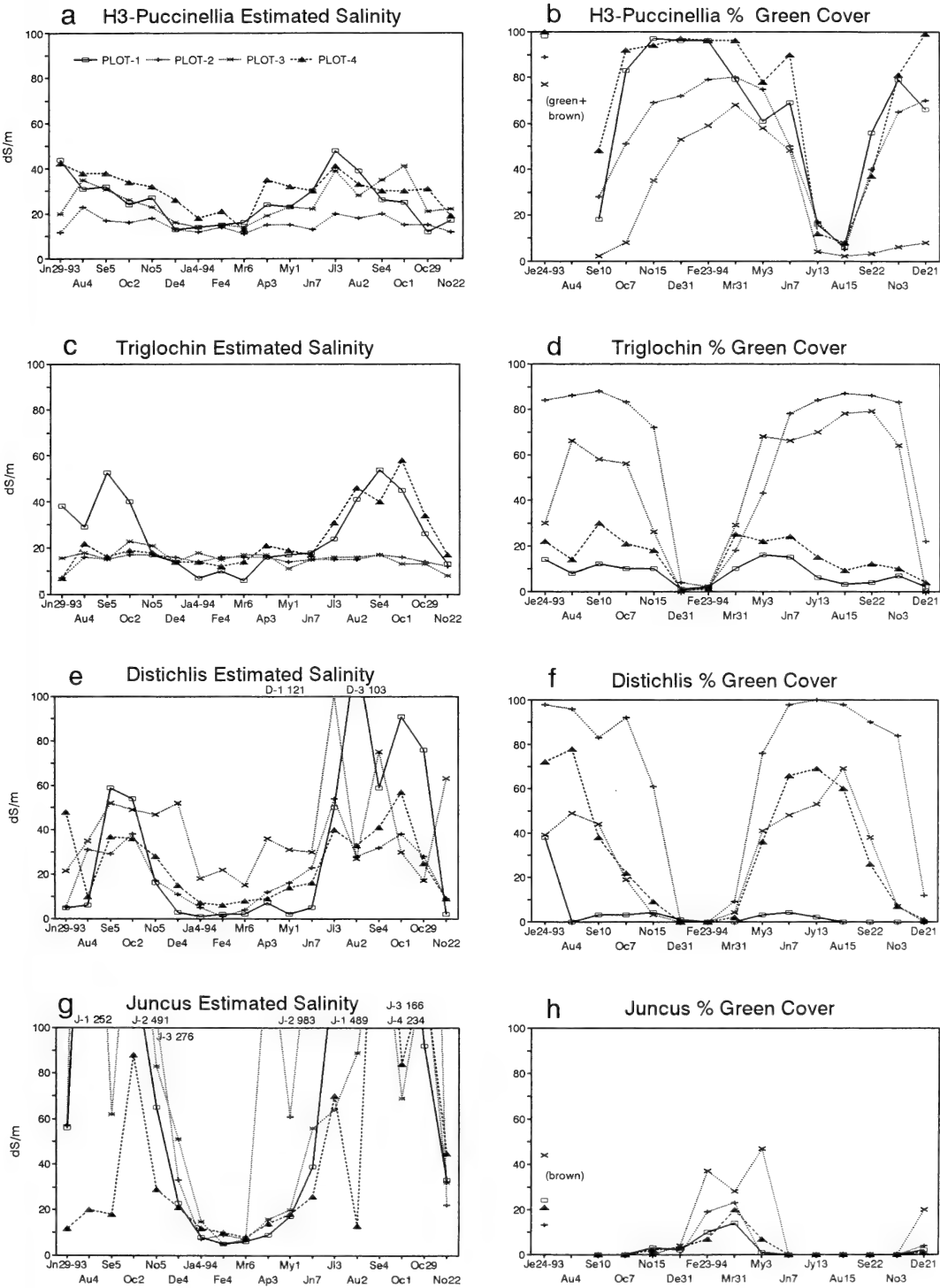
of the region. Growth occurs during the cool months, and seed is produced before a summer dormancy. However, regeneration by germination or resprouting often begins in advance of the fall rains. *Triglochin* (Fig. 4d) remains active through the summer, but declines during the cold months. Its succulent foliage is susceptible to damage from freezing. *Distichlis* (Fig. 4f) typically dies back completely during the cold months, but its preference for warm weather and its high salt tolerance (Ungar 1974; Hansen et al. 1976) enables it to grow on sites that during the summer become too saline for *Puccinellia*. Salt build-up in the *Juncus bufonius* plots (Fig. 4h) was more extreme than in the *Distichlis* plots. An early-flowering annual, *Juncus* can complete its life cycle within a short period of low salinity during winter and spring.

Though the ability of *Distichlis* to tolerate high salinity is by no means unique, its often greater

FIG. 4. Seasonal salinity and cover in sets of monitoring plots. a, b) H3-*Puccinellia* = high density, medium stature *Puccinellia howellii*. Reported conductivities are the saturated extract values adjusted for field moisture. Samples with accumulated salt produced artificial conductivity values that exceeded the level of a saturated solution (e.g., 226 dS/m at 20°C for NaCl), but which remained proportional to the salt content. 50 dS/m is approximately equivalent to coastal sea water. The unconnected cover values labeled "green + brown," and "brown" were measured at the end of the previous growing season.



Species Monitoring Plots - June 1993 to December 1994



capacity compared with other species has been noted in other settings. For example, in New England, *Distichlis* rapidly re-colonized bare patches of coastal salt marsh that were created by shading from wrack (Bertness et al. 1992; Shumway 1995). These areas then become hypersaline due to increased evaporation. Their studies suggest that *Distichlis* can invade and occupy patches too saline for the establishment and persistence of discrete individuals by transporting along its runners water and carbon from ramets outside the hypersaline zone.

The distribution of *Distichlis* within the salt springs seems to reflect not only its relatively high salt tolerance, but also a limited capacity for immersion. On both coasts *Distichlis* is a component of high marsh vegetation, where it is not subject to daily flooding (Macdonald and Barbour 1974; Silberhorn 1982; Macdonald 1988). In inland settings it is associated with only moderate moisture (Ungar 1974). The detrimental effect of inundation on *Distichlis*, and the associated abiotic factors, was demonstrated in a Louisiana tidal marsh undergoing vegetation decline associated with relative sea level rise. Webb et al. (1995) transplanted sod blocks of four species level with the marsh surface and raised 20 cm higher, equivalent to the level of a nearby healthy marsh. All species produced less biomass at the ambient level, but the greatest reduction was in those typically associated with high marsh habitat, a twenty-fold difference in the case of *Distichlis*. The poor growth at the ambient level was associated with negative substrate redox potential at both 2 cm and 15 cm depth. The elevated plantings had uniformly higher potentials, with oxidized conditions at 2 cm.

The comparatively larger number of plots assigned to monitor *Puccinellia*, and their division into stand categories, helped provide examples of the variation in growing conditions. The timing of *Puccinellia* germination appeared related to summer salinity. Seed in locations directly inundated by surface flow germinated as early as mid-summer, while areas with high summer salinity produced their major germination pulse in November or later. Locations with visible salt accumulation, including those near the evaporative edge of surface flows, seemed more prone to seedling mortality, and to the failure of tufts to regenerate in the fall.

The two *Puccinellia* plots located in the transplant area provided an example of salinity-related mortality, and evidence that the pattern of seepage can shift over time. During the first summer of monitoring, these high-density/high-stature stands had a measured salinity similar to *Distichlis* plots, and visible salt accumulation. At the same time, the plots were being invaded by *Distichlis*. The following fall, the *Puccinellia* tufts did not resprout, and though recruitment was heavy, little germination was recorded within the plot itself. In effect, the *Puccinellia* had regenerated, but had shifted in po-

sition, and was no longer centered within the plot boundaries. Toward the end of the monitoring period, plot H3-3 provided a similar example of non-regeneration due to shifting irrigation (Fig. 4b), however, the visible salt accumulation within the plot was not reflected in the soil samples collected from the periphery. Dense germination occurred outside and adjacent to the plot boundary, where surface flow was evident.

**Greenhouse.** The salinity preferences of *Puccinellia* are suggested by its behavior in the greenhouse. The greatest growth was seen in the group that remained at 20 dS/m. Growth at 60 dS/m was stunted, and 80 dS/m proved lethal. In the field, summer levels of 60 dS/m and higher were commonly found in the *Distichlis* and *Juncus* plots, and also in the plots of low-density/low-stature *Puccinellia*. The amount and rate of germination was inversely proportional to salinity, consistent with field observations that germination is delayed in areas that that accumulated salt during the previous summer.

#### CONCLUSIONS

The large majority of the *Puccinellia* cover was found in monotypic stands. The *Distichlis* stands were divided into two groups. The larger portion, two-thirds of the total cover, contained no *Puccinellia*, but often supported annual grasses during the cool season. The presence of *Puccinellia* in the remaining one-third and in the *Juncus* stands, might indicate locations where habitat conditions were intermediate or in flux.

The vegetation at the salt springs can be divided into two groups, based on the relative influence of spring discharge. A saline-winter/saline-summer division, typified by *Puccinellia* and *Triglochin*, tends to be wet year-round. The habitat remains saline during the rainy season, excluding glycophytes during the period of active *Puccinellia* growth. Salinity rises only moderately during the summer, permitting late-summer to early-fall germination by *Puccinellia*. A fresh-winter/saline-summer division, typified by *Distichlis* and *Juncus*, is more likely to occur at the periphery or at elevated areas within the springs, where the influence of the discharge is less direct. During the summer, wicking and evaporation promote hypersalinity, but winter precipitation dilutes the salt sufficiently to permit the growth of glycophytes. The areas occupied by these vegetation types may shift somewhat over time in response to changes in the pattern of seepage and surface flow.

This study concludes that a major requirement for *Puccinellia*, apart from suitable salinity, is a volume of spring discharge sufficient to maintain salinity during both the wet and dry seasons. In this region of relatively high precipitation, few salt springs may meet this requirement, but qualifying sites merit attention because they may harbor un-

documented populations or could become candidate sites for outplanting. The evidence that *Puccinellia* and *Distichlis* have different hydrologic preferences provides useful information for managing the only known population of *Puccinellia* in the presence of *Distichlis*. For instance, *Distichlis* might be excluded by lowering the grade sufficiently so that surface flow occurs year-round. This approach is currently being explored by CalTrans within the area of their transplant project.

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## SPHAGNUM BALTICUM IN A SOUTHERN ROCKY MOUNTAIN IRON FEN

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*Sphagnum balticum* (Russow) C. Jensen is a widespread Holarctic peat moss of raised and blanket bogs, occurring partly or completely submerged in pools, in floating mats and on hummocks. It is known from arctic and subarctic Greenland, North America (Crum and Andersen 1981; Crum 1984), Scandinavia, the British Isles, Russia and northern China. It is one of the rarest plants in the United Kingdom (UK Biodiversity Group 1998). Until now, the known range of *S. balticum* in North America extended south to about 57 degrees north latitude in western and central Canada and it is unknown in the lower 48 United States. Therefore, it is striking to discover this species in the San Juan Mountains in southwestern Colorado disjunct by more than 2000 km from the main range of the species in northern Canada and Alaska (*Sphagnum balticum*, Cooper #2281, COLO, BING).

During a regional analysis of iron fens, we found *Sphagnum balticum* in the Chattanooga iron fen (2990 m elevation, Latitude 37°50'N, Longitude 107°43'W) south of Red Mountain Pass where it is the most abundant moss in shallow pools, growing with the sedges *Carex aquatilis* Wahlenberg and *C. utriculata* Boott. It is easily separated in the field from the only other *Sphagnum* in section Cuspidata present in the area, *S. angustifolium* (Russow) C. Jens. by a laxer habit and conspicuous lingulate and spreading stem leaves. The fen is almost completely covered by *Sphagnum* mats and hummocks, with abundant *S. angustifolium*, *S. russowii* Warnst., *S. fuscum* (Schimp.) Klinggr. and *S. fimbriatum* Wils. (nomenclature follows Crum 1984). We found *S. girgensohnii* Russow, another new Colorado record, in a different iron fen.

The water and soil in most *Sphagnum*-dominated peatlands is acidic. The origin of the acids has been linked to *Sphagnum* cation exchange capacity (Clymo 1963; Clymo and Hayward 1982; Glaser 1987), atmospheric acid deposition (Gorham 1967), biological uptake of nutrient cations by plants (Mitsch and Gosselink 1994), and the buildup of organic acids by decomposition (Gorham et al. 1984). These processes control autochthonous production and accumulation of acids in ombrogenous peat-

lands (bogs). Fens in the Rocky Mountains, however are soligenous (formed on slopes) or limnogenous (formed on lake margins), and are seasonally flushed with abundant snow melt water (Cooper and Andrus 1994). Because strong flushing occurs, the pH of surface and ground water is controlled by the chemistry of watershed surface and ground waters, not autochthonous acid production.

Warm and dry summers with long rainless periods and a large evaporative demand are characteristic of the continental climate of the southern Rocky Mountains. Peatlands occur only where a continuous supply of ground water maintains perennially saturated soil conditions. The most common peatlands are transitional fens with slightly acid waters in mountain ranges of granite, rhyolite or metamorphic bedrock (Cooper and Andrus 1994) and extreme rich fens with circumneutral or basic waters in areas of, limestone, dolomite, shale, and basalt bedrock (Cooper 1996).

Colorado iron fens appear to be geochemically unique and occur in areas with highly mineralized outcrops, such as occur on Red Mountain Pass. While iron fens are hydrologically similar to other Colorado fens, with ground water discharge permanently saturating valley bottom wetlands, the source water flows through fractured iron pyrite-rich bedrock and talus, oxidizing pyrite and forming sulfuric acid.

Chattanooga iron fen surface water has a pH from 3.8 to 4.4, similar to bogs and poor fens in northern Minnesota (Glaser 1987). Acid drainage from historical metal mines in Colorado produces similar low pH waters, and pollutes some Colorado wetlands (Arp et al. 1999), however iron fens are natural ecosystems. Although geochemical processes external to the peatland generate the acids in iron fens, the fen flora is limited to acid tolerant species that also occur in poor fens and bogs.

Bog waters have low ion concentrations because precipitation is the primary water supply. In contrast, iron fens have high ion concentrations because sulfuric acid produced in the watershed leaches and mobilizes metal and base cations from rock. Concentrations of  $\text{Ca}^{2+}$  in Chattanooga fen

surface water range from 14–20 mg/liter, and  $\text{SO}_4$  averages 117 mg/liter.  $\text{Ca}^{2+}$  concentration in bogs range from 0.5 to 2.0 mg/liter (Glaser et al. 1981, 1990), in poor fens from 2.0–5.0 mg/liter (Sjörs 1963; Glaser et al. 1981), transitional fens in the Rocky Mountains from 2.0–7.0 mg/liter (Cooper and Andrus 1994), and rich fens from 5.0–30.0 mg/liter (Glaser et al. 1981, 1990). Thus, the Chattanooga iron fen has  $\text{Ca}^{2+}$  concentration most similar to a rich fen. High iron concentrations (0.2–6.3 mg/liter) precipitate onto fen organic matter forming terraced bog iron ore (limonite) deposits (Harrer and Tesch 1959), which are characteristic of iron fens. Limonite terraces perch the water table and form extensive networks of pools and ponds that are uncommon in most other Colorado fens.

The presence of plants, such as *Sphagnum balticum*, that are widely disjunct from their main ranges has always intrigued biogeographers. Did people, migratory birds or other vectors transport these plants? Are they the last vestiges of plant populations that established in the southern Rocky Mountains from the north during the Pleistocene as suggested by Hooker and Gray (1880)? Or do they reflect much older plant evolutionary and developmental patterns as suggested by Weber (1965)?

It is unlikely that animals, people or wind would have dispersed *Sphagnum balticum*, and Colorado has numerous other boreal montane bryophytes and lichens that exist in tiny populations disjunct from their main ranges in the boreal and subarctic regions of North America. Examples include *Cladina stellaris* (Opiz) Brodo found in a few 10 m<sup>2</sup> patches on the margin of a fen in the Tarryall Range, *Sphagnum platyphyllum* (Braithwaite) Warnstorf in two small wetlands in the Sawatch Range, *S. contortum* Schultz in one small wetland in the Front Range, *Paludella squarrosa* (Hedwig) Bridel in a couple of tiny alpine wetlands on Guanella Pass, and *Scorpidium scorpioides* (Hedwig) Limpricht in a few acres of calcareous fen in South Park (Cooper 1991; Weber and Wittmann 1996). The large number of species persisting as localized populations, many found in only one fen, or on one mountain slope, suggests that these populations are the vestiges of what may have been wider distributions along the Cordillera that are much older than the Pleistocene. Many Colorado fens have basal <sup>14</sup>C dates of 10,000–12,000 years BP (Cooper 1990; Chimner and Cooper 2002), with peat body initiation soon after the melting of Pleistocene glaciers. Boreal montane species could have found stable refugia in the southern Rocky Mountains and persisted through the Holocene.

It is striking that new populations of widespread and well-known boreal montane plants are still being found in Colorado, a state with modern floristic manuals (e.g., Weber and Wittmann 2001), numerous botanists, and a rich history of botanical investigation. It indicates that additional species are likely to be discovered. Rare plants, such as *S. balti-*

*cum*, occur in very specialized habitats, such as iron fens, that are difficult to find. Careful inventories are necessary to make certain that logging, mining, and recreation and water developments do not inadvertently destroy the only populations of species occurring in the southern Rocky Mountains, and that may have existed here for many millennia. It also indicates the sensitivity of these habitats and populations to hydrologic variability that could accompany human induced climate changes. Since populations of these species are very small and the circumstances of survival of each species are likely to be unique, there is no chance for species replenishment.

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## EVIDENCE OF A NOVEL LINEAGE WITHIN THE *PONDEROSAE*

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### ABSTRACT

Phylogenetic analysis of the DNA of a putative portion of the nuclear NADH-specific nitrate reductase gene revealed the existence of a *Pinus jeffreyi* lineage that gave rise to *P. washoensis* and the North Plateau race of *P. ponderosa* var. *ponderosa*. These data are consistent with Lauria's (1991) hypotheses that the North Plateau race is genetically distinct from the other races of the species, and that this race should be considered conspecific with *P. washoensis*.

*Pinus* subsection *Ponderosae* is an economically important and well-represented group across much of western North America. However, the species in this group have been the source of considerable taxonomic disagreement (Lauria 1991, 1997; Kral 1993; Rehfeldt 1999). Taxonomic treatments and inferences about the evolution of the *Ponderosae* have been based on a large number of different data sets, including quantitative morphological characters (Peloquin 1984; Rehfeldt et al. 1996; Rehfeldt 1999), terpene chemistry (Mirov 1961; Smith 1964, 1967, 1977; von Rudloff and Lapp 1991), isozymes (Niebling and Conkle 1990), crossability (Critchfield 1984), provenance analysis (Wells 1964; van Haverbeke 1986), and the fossil record (Stockey 1984; Axelrod 1986). Some of these studies have produced conflicting data or additional uncertainty because of the omission of key species or varieties (Lauria 1991).

The primary objective of this limited study was to test two of Lauria's hypotheses: (1) the North Plateau race of ponderosa pine (*Pinus ponderosa* Douglas ex Lawson and C. Lawson) is a distinct genetic entity relative to the other races of this species (Lauria 1991); and (2) Washoe pine (*Pinus washoensis* Mason and Stockwell) and the North Plateau race of ponderosa pine are conspecific (Lauria 1997). Sampling thus focused primarily on the five geographic races of ponderosa pine (Smith 1977; Conkle and Critchfield 1988), Washoe pine, and Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.). Three other members of *Ponderosae*, *Pinus arizonica* Engelm. and Martinez, *Pinus durangensis* Martinez, and *Pinus engelmannii* Carr., were included for comparison of relative genetic divergence. *Pinus coulteri* D. Don from subsection *Sabinianae* was also included because of its high crossability with Jeffrey pine (Zobel 1951) and the close relationship between subsections *Sabinianae* and *Ponderosae* exhibited in a chloroplast DNA analysis

(Kupkin et al. 1996). *Pinus contorta* Dougl. ex Loud. was included as an outgroup. Most taxa were represented by two samples; however four samples from the North Plateau race and one sample from each of the three recognized populations of Washoe pine were included (Table 1). This study was conducted concurrently with a larger ecological genetics study (Rehfeldt 1999) of Washoe pine, Jeffrey pine, and ponderosa pine.

DNA was isolated from needle tissue according to Lodhi et al. (1994). PCR products were generated using primers designed to target a region coding for the two hinges that connect the internal heme domain to the amino and carboxy terminal domains of the nuclear NADH-specific nitrate reductase (NADH-NR) gene (Zhou et al. 1995; Patten 1999). Manual sequencing of the PCR product was conducted using the USB Sequenase Kit (Amersham). A BLAST search of the GenBank data base did not reveal a match between our sequences and those reported as NADH-NR. However, the sequence and structure of nitrate reductase is not known for any gymnosperm. Furthermore, the PCR primers are targeted to an area known to contain introns (Zhou and Kleinohs 1996), lessening the chance of similarity to pine. Thus, to be conservative, the sequences might best be considered anonymous, although the parsimonious distribution of synapomorphies strongly suggests the sequences are orthologous (Fig. 1). Paralogous PCR products would likely exhibit a more random distribution with respect to taxonomic classification and geography (see below).

Because there were variable amounts of missing data at the termini of the PCR products, a 287-bp fragment was used in the final phylogenetic analysis. The sequences were analyzed using PAUP version 3.1.1 (Swofford 1993). The branch and bound exact algorithm was used and two most parsimonious trees were recovered. These differed only in the resolution of one dichotomy. Both trees had a length of 25 and a consistency index of 0.90. A consensus tree was constructed and all branches of zero length were collapsed (Fig. 1).

This phylogenetic analysis offers novel insights

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The results of the phylogenetic analysis also suggest that Washoe pine and the North Plateau race of ponderosa pine form a robust clade (bootstrap 100%), within which both taxa are polyphyletic (Fig. 1). The putative NADH-NR sequences from these samples appear to represent four alleles distributed randomly among six populations. Due to



the small sample size, it cannot be determined how these alleles are structured within or among populations or species. Expanded studies using additional informative DNA regions and statistically-significant intrapopulation sampling are needed. Regardless, the random distribution of alleles is consistent with the close relationship or even conspecific status previously proposed between Washoe pine and the North Plateau race (Wells 1964; Haller 1965; Critchfield 1984; Niebling and Conkle 1990; Lauria 1991, 1997; Brayshaw 1996; Rehfeldt 1999). Provenance tests by Wells (1964) showed that Washoe pine was more similar to the North Plateau race than it was to the Pacific race of *ponderosa* pine. Critchfield (1984) proposed that Washoe pine could be a recent derivative of the North Plateau race. This view is consistent with a close relationship inferred from isozyme data (Niebling and Conkle 1990). Washoe pine and the North Plateau race were found to have a genetic distance of 0.004, a value nearly identical to the genetic distance found among the three recognized populations of Washoe pine. Furthermore, Rehfeldt's (1999) quantitative analysis of adaptive traits determined that Washoe pine and the North Plateau race of *ponderosa* pine are very closely related. Based on his and previous research, Rehfeldt (1999) concluded that these taxa should be considered synonymous.

The high level of divergence of the Washoe/North Plateau clade (seven synapomorphies and two deletions) suggests an origin involving small population size and isolation. The divergent Washoe pine/North Plateau clade eventually came to occupy the Willamette Valley and the region approximating the current extent of the maritime climate east of the Cascade crest. Members of this clade dispersed as far east as the Continental Divide, where an abrupt genetic transition is evident. Latta and Mitton (1999) found a steep east-west cline in cpDNA and mtDNA, consistent with secondary contact between diverged taxa. Similarly, Critchfield (1984) previously proposed that Washoe pine expanded over the Pacific Northwest only to be later absorbed by the North Plateau race of *ponderosa* pine.

This study includes a single tree from a population on the Fort Lewis plains of the Puget Sound. This population is isolated from the North Plateau race by the Cascade mountains. Our DNA sequence from this individual is identical to that of *Ponderosae* found in the Rocky Mountains, Sierra Madre, and Sierra Nevada, suggesting that *ponderosa* pine from the Puget Sound region could be a relictual population of formerly widespread *P. ponderosa* s.l. This is in no way conclusive, as a single DNA marker from a single specimen may not be representative of a population. Nevertheless, it does suggest that the genetics of *Ponderosae* in the Puget Sound area needs to be investigated in detail as numerous studies have hypothesized that the Puget Sound region was a glacial (Pleistocene) refugium

for numerous plants and animals (e.g., Harris 1965; Steinhoff et al. 1983; Heusser 1985; Soltis et al. 1997).

This study does not support the traditional varietal classification of *ponderosa* pine (e.g., Conkle and Critchfield 1988). Variety *scopulorum*, the Rocky Mountain form, is not distinct in our analysis from the Pacific and the Southern California races of var. *ponderosa*. The principal finding of this phylogenetic analysis is the existence of a *P. jeffreyi* lineage that gave rise to Washoe pine and the North Plateau race of var. *ponderosa*, a race that appears to be fundamentally distinct from the remainder of *P. ponderosa* s.l. Our results cannot confirm conspecificity of Washoe pine and the North Plateau race of *ponderosa* pine, but do indicate a very close relationship of these taxa to each other and to Jeffrey pine. This study did not lend insights into the relationships among the southwestern and Mexican species of subsection *Ponderosae*, suggesting relatively little genetic divergence of these taxa compared to the *P. jeffreyi* lineage. However, morphological and ecological data (e.g., Peloquin 1984; Rehfeldt et al. 1996) indicate the existence of significant patterns of genetic divergence in the *Ponderosae* of the southwestern U.S. and Mexico. We hope that this note provides the impetus for a more detailed phylogenetic study of the subsection *Ponderosae*. Larger sample sizes and multiple, rapidly-evolving DNA segments should be analyzed to test the results reported here.

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# NOTEWORTHY COLLECTIONS

## ALASKA

*ALLIARIA PETIOLATA* (Bieb.) Cavara & Grande (BRAS-SICACEAE).—City and Borough of Juneau, Alaska, in the landscaped area next to a parking lot near the intersection of Village and Wittier streets, 58°18'05"N, 134°24'53"W, 6 June 2001. One mature, flowering plant was found by P. Johnson and removed before it set seed. It is unclear how this plant arrived at this urban area. It is unlikely that it was introduced by the landscaping activities since there had been no recent additions of plants or soil.

*Previous knowledge.* Native to northern Europe. Commonly called garlic mustard because of the characteristic smell of its leaves when crushed, it is a highly competitive, aggressive herbaceous invader that forms dense understory populations. Present in 34 USA states (<http://plants.usda.gov>), particularly in the eastern USA (Rollins, R.C., *The Cruciferae of Continental North America*. 1993. Stanford University Press) and the four Canadian provinces of British Columbia, New Brunswick, Ontario, and Quebec (<http://infoweb.magi.com/~ehaber/ipcan.html>). The previously known British Columbia collections were near Vancouver and Vernon (E. Haber personal communication).

*Significance.* First record in Alaska. The previously known sites in British Columbia are approximately 1300 km to the southeast. *Alliaria petiolata* is one of the most pestiferous non-native invasive species of forest understoreies in the USA and Canada. It can form monospecific stands, exclude native communities, and be essentially impossible to eradicate once it is established. While it was originally believed this plant was the only individual growing in Alaska, P. Johnson subsequently found a large population of plants nearby. Although the early detection of this plant has been important, it is unclear whether the population can be successfully eradicated. The specimen has been placed in the Herbarium at the University of California, Davis (DAV).

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## CALIFORNIA

*DROSERA ALICIAE* Hamet (DROSERACEAE).—Mendocino county, CA, 39°15'N, 123°45'W, elevation 160 m, 2 November 1997. A few hundred meters west of Albion Little River Road, just south of the County Airport. A single spreading colony of plants was found in wet depressions and *Sphagnum* mounds in a pine/cypress pygmy forest.

*Previous knowledge.* Native to South Africa, *Drosera aliciae* is a plant commonly grown by carnivorous plant enthusiasts.

*Significance.* It has not previously been collected in California, and is probably a new introduction for North America. This plant was introduced by horticulturists with

a number of other carnivorous plant taxa. It was reproducing both vegetatively and by seed. A more complete discussion is given under the *Drosera capensis* collection description. A specimen has been placed in the Herbarium at the University of California, Davis, #MR971101.

*DROSERA CAPENSIS* L. (DROSERACEAE).—Mendocino county, CA, 39°15'N, 123°45'W, elevation 160 m, 2 November 1997. A few hundred meters west of Albion Little River Road, just south of the County Airport. Large colonies of plants were found growing in wet depressions and *Sphagnum* mounds in a pine/cypress pygmy forest.

*Previous knowledge.* Native to South Africa, *Drosera capensis* is a common greenhouse weed in collections where carnivorous plants are grown. It is not listed in the various floristic works of California. The Jepson Manual notes the presence of *D. linearis* Goldie in Mendocino County, but this is probably an erroneous reference to observations of *D. capensis*. A North American *Drosera* species, *D. linearis* does resemble *D. capensis*, but *D. linearis* is extremely difficult to cultivate and is nearly absent from most collections. As such it is unlikely any horticulturists have ever planted out *D. linearis* in California. *D. linearis* grows in Canada from Labrador west to Ontario, and in the US in Minnesota, Wisconsin, Michigan, and Maine. No plants of *D. linearis* were found in the area.

*Significance.* This cluster of wildland locations has been used by carnivorous plant horticulturists for introduction experiments since the 1970s (P. D'Amato, *Carnivorous Plant Newsletter*, 1988, 17: 15–21). Plants from nearly every carnivorous genus have been planted over the years, but most died within a few years. Non-native species that persisted and were spreading by seed or vegetative means were *Drosera aliciae*, *D. binata*, *D. capensis*, *D. capillaris*, *D. filiformis*, *D. intermedia*, *D. nitidula* × *occidentalis*, *Sarracenia flava*, *S. leucophylla*, *S. minor*, *S. purpurea*, *S. rubra*, many interspecific *Sarracenia* hybrids, and *Utricularia subulata*. Additional species present but which may be waifs were *Dionaea muscipula*, *Drosera burmannii*, *D. slackii*, *Pinguicula lusitanica*, and *Utricularia gibba*. None of these plants are included in Californian floristic works except for *Darlingtonia californica*, *Drosera capensis* (incorrectly listed in The Jepson Manual as *D. linearis*), *D. filiformis*, *Sarracenia purpurea*, and *Utricularia gibba*. *Darlingtonia californica* was abundant although it is not native to this location—its nearest natural occurrence is in central Trinity County (J. H. Rondeau, *Carnivorous Plants of California*, 1991, unpublished manuscript). Many of the clumps of this plant were heavily damaged by infestations of greenhouse thrips, a condition not seen in natural populations. The only thriving species were *Darlingtonia californica*, *Drosera capensis*, and *Utricularia subulata*. Although it is unlikely any of these plants will spread from these isolated plantings, *Drosera capensis* or *Utricularia subulata* (which reproduce both vegetatively and by copious seed production) would be difficult to eradicate if they invaded other high quality natural habitats. The only carnivorous plant native to the site is *Drosera rotundifolia*. Those familiar with the site believe the *Drosera rotundifolia* is being displaced by the exotic species (C. Gardner personal communication).

Specimens have been placed in the Herbarium at the University of California, Davis, #MR971103.

*UTRICULARIA SUBULATA* L. (LENTIBULARIACEAE).—Mendocino county, CA, 39°15'N, 123°45'W, elevation 160 m, 2 November 1997. A few hundred meters west of Albion Little River Road, just south of the County Airport. Large colonies of plants were found in wet depressions and water drainages in a pine/cypress pygmy forest.

*Previous knowledge.* This is a widespread species found on every continent except Antarctica. In the United States it is found on the Atlantic and Gulf coasts from Massachusetts to Florida to Texas, and inland to Arkansas and Tennessee (P. Taylor, *The Genus Utricularia: a Taxonomic Monograph*, 1989, Kew Bulletin Additional Series XIV). It is a common greenhouse weed in collections of carnivorous plants.

*Significance.* A first collection for California. The plants were growing in densely matted clumps and were reproducing vegetatively and by seed. Both cleistogamous and chasmogamous flowers were present. Unless deliberately spread, it is unlikely this plant will escape from these plantings, but if it did it would be difficult to eradicate. *Utricularia gibba* (probably introduced) was also present in flower. A more complete discussion is given under the *Drosera capensis* collection description. A specimen of *U. subulata* has been placed in the Herbarium at the University of California, Davis, #MR971102.

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#### OREGON

*AGROSTIS HOWELLII* Scribn. (POACEAE).—Linn Co., rare, N-sloping bench in a moist *Acer circinatum*-*Carex deweyana* community, Coburg Hills, 25 km NE of Eugene, T15S R2W S9, elev. 450 m, 3 Oct 1995, Brainerd 42 (OSC) (! K. L. Chambers 1996 OSC).

*Previous knowledge.* Previously known as a narrow endemic from a few sites on the south side of the Columbia River Gorge in northern Oregon.

*Significance.* Circa 165 km SSW of previously documented populations.

*CAREX SCIRPOIDEA* Michx. subsp. *STENOCHLAENA* (Holm) A. Löve & D. Löve (CYPERACEAE).—Lane Co., dripping cliff with *Salix sitchensis*, *Agrostis*, above Forest Service Road 19, near Cougar Dam, T16S R5E S31, elev. 520 m, 15 Jul 1998, Newhouse 98027 (MICH, OSC, WTU) (! A. A. Reznicek 2001 MICH).

*Previous knowledge.* Ledger sedge ranges from Alaska south to Washington and Montana.

*Significance.* First record for this subspecies in Oregon.

*DAPHNE LAUREOLA* L. (THYMELAEACEAE).—Lane Co., Laurelwood golf course, Eugene, elev. 215 m, 13 Feb 1998, Newhouse 98002 (OSC); Hawkins Heights, Eugene, elev. 215 m, 20 Feb 1998, Newhouse 98003 (OSC); Masonic Cemetery, Eugene, elev. 150 m, Aug 1997, Newhouse 97051 (OSC).

*Previous knowledge.* Spurge-laurel is native to Europe,

and adventive in British Columbia and western Washington, where it is bird-disseminated.

*Significance.* First report as an escape from cultivation in Oregon.

*GALIUM PEDMONTANUM* (Bellardi) All. (RUBIACEAE).—Benton Co., common in disturbed meadow 0.5 km NW of Pigeon Butte, elev. 80 m, T13S R5W S32, 5 Jun 1993, Zika 12025 (OSC, WTU).

*Previous knowledge.* Mountain crosswort is native to the Mediterranean, and adventive in Idaho, Montana, and in the southeastern United States.

*Significance.* First Oregon report; discovered by Robert Frenkel in 1992.

*PETASITES FRAGRANS* (Vill.) C. Presl (ASTERACEAE).—Benton Co., steep forested bank on W shore of Willamette River, Corvallis, elev. 60 m, T12S R5W S2, 3 Feb 1999, Zika 13717 (OSC, US, WTU); same site, 15 Mar 2000, Zika 14848 (OSC).

*Previous knowledge.* Winter heliotrope is native to N Africa, and occasionally planted as an ornamental in western Oregon.

*Significance.* First report of an escape from cultivation in Oregon.

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#### OREGON

*ACAENA NOVAE-ZELANDIAE* Kirk (ROSACEAE).—Coos Co., Randolph Road, near Route 101, 6 km N of Bandon, common weed on sandy banks, roadbeds, dikes, and cranberry fields, with *Crepis capillaris*, *Hypericum boreale*, *Juncus planifolius*, *J. canadensis*, *Poa annua*, elev. 52 m, T28S R14W S4, 7 Sep 1999, Zika 14247 (OSC, WTU); Curry Co., Gold Beach, 13 Aug 1951, Jenkins s.n. (OSC); adventive on Azalea Lane, Wedderburn, elev. 30 m, T36S R15W S25, 7 Jun 2000, Stansell 3196 (OSC); lawn weed, Route 101, Gold Beach Ranger Station, Gold Beach, T37S R15W S1, 17 Aug 2000, Stansell 3201 (OSC).

*Previous knowledge.* Biddy-biddy is native to New Zealand, and occasionally cultivated as a ground cover. It readily spreads via barbed fruits. *Acaena* is classified as a noxious weed in California, where it is found on disturbed ground along the coast. In Oregon it has been observed at several sites in addition to the ones vouchered, including a large population at Cape Blanco lighthouse in Curry Co.

*Significance.* First report for Oregon. We first observed *Acaena* in June 1992 at the U.S. Forest Service office in Gold Beach, where lawn mowers scattered the seeds and led to an increase in the population. The Oregon Dept. of Agriculture has made several unsuccessful attempts to extirpate the species with herbicides, starting in 1997.

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## OREGON

*CERASTIUM PUMILUM* Curtis (CARYOPHYLLACEAE).—Jackson Co., pasture with vernal pools, Route 234 E of Sams Valley, 12 May 1974, *Chambers 3974* (OSC, WTU); Multnomah Co., silty shore, delta of Sandy River, elev. 4 m, 16 Apr 1992, *Zika 11470* (OSC, WTU), *Zika 11480* (WTU).

*Previous knowledge.* Dwarf mouse-ear is native to Europe, and naturalized in eastern North America as well as British Columbia. In the Pacific Northwest often growing among and confused with *C. semidecandrum* L.

*Significance.* First report for Oregon.

*COTONEASTER DIVARICATUS* Rehder & E.H. Wilson (ROSACEAE).—Lane Co., bird-sown in thicket with *Quercus garryana*, *Toxicodendron*, Morse Ranch Park, Eugene, 30 Apr 1998, *Love 9816* (OSC).

*Previous knowledge.* Spreading cotoneaster is native to central China, and cultivated as an ornamental in the Pacific Northwest.

*Significance.* First collection of an escape from cultivation in Oregon.

*COTONEASTER INDURATUS* J. Fryer & B. Hylmö (ROSACEAE).—Lane Co., thickets, near Willow Creek, West Eugene, elev. 122 m, 28 May 1992, *Zika 11593* (WTU); same population, 8 Jul 1997, *Zika 13231* (WTU).

*Significance.* First reports for hard cotoneaster as an escape from cultivation. Specimens identified by Jeanette Fryer.

*SORBUS CALIFORNICA* Greene (CAPRIFOLIACEAE).—Klamath Co., Rim above Crater Lake, 12 Aug 1919, *Sweetser s.n.* (ORE); same site, elev. 2150 m, 13 Jul 1929, *Wynd 1533* (ORE); Wizard Island, Crater Lake, 28 Jun 1934, *Applegate 8977* (OSC); Phantom Ship, Crater Lake, elev. 1885 m, *Zika 12516* (OSC).

*Significance.* First collections for Oregon. All sites are in Crater Lake National Park.

*VERONICA VERNA* L. (SCROPHULARIACEAE).—Union Co., sunny opening, Route 82 beside Wallowa River, 6 km SE of Minam, elev. 825 m, 2 Jun 1961, *Mason 1142* (ORE); dirt road, Miller Flat, W shore of Wallow River, elev. 750 m, 21 May 1994, *Zika 12182* (OSC); Wallowa Co., dirt road 11 km W of Enterprise, elev. 1220 m, 24 Apr 1961, *Mason 807AA* (OSC); 7 miles basalt cliff, Wallowa Falls, elev. 1525 m, 24 Jun 1962, *Mason 5051* (OSC); Buck Creek near Imnaha River, elev. 580 m, 7 May 1991, *Zika 11089* (OSC).

*Previous knowledge.* Spring speedwell is native to Europe. Crins et al. (Michigan Botanist 26: 161–166, 1987) discuss how to separate it from *V. arvensis*. Mason (1980, Guide to the Plants of the Wallowa Mountains of Northwestern Oregon, Museum of Natural History, Univ. of Oregon, Eugene) reported her collections of *V. verna* as *V. triphyllus*. The latter has lower leaves palmately lobed, and bracts shorter than fruiting pedicels. *Veronica verna* has pinnately lobed lower leaves and bracts longer than the fruiting pedicels.

*Significance.* First documentation in Oregon.

## WASHINGTON

*CARDAMINE FLEXUOSA* With. (BRASSICACEAE).—Grays Harbor Co., moist ground, edge of building, near

mouth of Boone Creek, elev. 5 m, 13 Dec 2001, *Zika 16733* (WTU); King Co., wet sunny ditch, Burke Gilman Trail 2.4 km N of Matthews Beach, Lake City, Seattle, elev. 10 m, 30 Aug 2001, *Zika 16467* & *Jacobson* (WTU); weed in garden bed, Madison Park, Seattle, elev. 10 m, 31 Aug 2001, *Zika 16474* (WTU); San Juan Co., wet ground in shade of *Alnus rubra*, Mineral Point, San Juan Island, elev. 5 m, 27 Oct 2001, *Zika 16708A* (WTU).

*Significance.* First report for Washington for this Eurasian native.

*CERASTIUM PUMILUM* Curtis (CARYOPHYLLACEAE).—Island Co., dunes near W shore of Cranberry Lake, Whidby Island, elev. 3 m, 20 May 2000, *Zika 15000A* (WTU); King Co., cracks in asphalt sidewalk, Montlake, Seattle, elev. 15 m, 20 May 2000, *Zika 14998* (WTU); San Juan Co., Turn Point, San Juan Island, 4 Apr 1992, *Atkinson 307* (WTU); sand, Spencer Spit, Lopez Island, elev. 2 m, 21 May 2000, *Zika 15005* (WTU).

*Significance.* First report for Washington.

*COTONEASTER DIVARICATUS* Rehder & E.H. Wilson (ROSACEAE).—King Co., bird-sown in thickets, with *Corylus cornuta*, *Gaultheria shallon*, arboretum, near Union Bay, Seattle, elev. 20 m, 15 Sep 1999, *Zika 14332* & *Jacobson* (WTU); same population, 26 Oct 2000, *Zika 15609* (WTU; dupl. det. by Bertil Hylmö).

*Significance.* First collection of an escape from cultivation.

*COTONEASTER LUCIDUS* Schldtl. (ROSACEAE).—Columbia Co., spreading and naturalized in Tucannon River bottomland, T9N R41E S30, elev. 1045 m, 27 Jun 1989, *Urban 89-001* (OSC).

*Previous knowledge.* Shiny cotoneaster is native to Siberia and Mongolia. It is occasionally cultivated in the Pacific Northwest, often under the misapplied name *C. acutifolius* Turcz.

*Significance.* First collection of an escape from cultivation.

*COTONEASTER NITENS* Rehder & E.H. Wilson (ROSACEAE).—King Co., thickets, partial shade, campus of Univ. of Washington, Seattle, elev. 25 m, 26 Oct 1999, *Zika 14660* & *Jacobson* (WTU); same population, 6 Nov 2000, *Zika 15645* (WTU).

*Previous knowledge.* Few-flowered cotoneaster is native to western China, and an uncommon ornamental in western Washington.

*Significance.* First collection of an escape from cultivation.

*COTONEASTER SALICIFOLIUS* Franch. (ROSACEAE).—King Co., spreading from cultivation to thickets, Kubota Gardens, Rainier Beach, Seattle, elev. 50 m, 3 Nov 1999, *Zika 14704* (WTU); bird-sown in thickets, campus of Univ. of Washington, Seattle, elev. 25 m, 7 Nov 1999, *Zika 14708* (WTU); bird-sown, partial shade, Madrona, Seattle, elev. 50 m, 2 Aug 2000, *Zika 15187* (WTU); cracks in concrete wall, ship canal near Portage Bay, Seattle, elev. 6 m, 7 Nov 2000, *Zika 15655* (WTU).

*Previous knowledge.* Willow-leaved cotoneaster is native to western China, and planted as an ornamental in western Washington for its brilliant autumn fruits. American robins (*Turdus migratorius*) and American crows (*Corvus brachyrhynchos*) eat the fruit and disperse the seed.

*Significance.* First collections for Washington as an escape from cultivation.

*COTONEASTER TENGUYEHENSIS* J. Fryer & B. Hylmö (ROSACEAE).—King Co., thickets near Washington Park, Seattle, elev. 35 m, 15 Sep 2000, *Zika* 15482 (WTU); slope near small creek, Washington Park arboretum, Seattle, elev. 20 m, 2 Nov 2000, *Zika* 15630 (WTU).

*Previous knowledge.* Tengyueh cotoneaster is native to SW China, and an uncommon ornamental in western Washington.

*Significance.* First report of an escape from cultivation in Washington.

*CREPIS SETOSA* Haller f. (ASTERACEAE).—Clark Co., grassy roadside near Loop Road, elev. 10 m, 24 Jul 2000, *Zika* 15114A & Weinmann (WTU); lawn weed by soccer field, NE18th St., elev. 90 m, 14 Sep 2001, *Zika* 16558 (WTU).

*Significance.* First collections in Washington for this southern European native.

*CYPERUS DIFFORMIS* L. (CYPERACEAE).—Franklin Co., sandy E shore of free-flowing Columbia River, elev. 100 m, T10N R28E S1, 2 Oct 2001, *Zika* 16671 (EIU, MICH, WS, WTU).

*Significance.* First report for Washington for this Asian native.

*FRAXINUS PENNSYLVANICA* Marsh. (OLEACEAE).—Grant Co., low ground between dunes, near Potholes Wildlife Area, SW of Moses Lake, elev. ca. 330 m, 14 Jun 2001, *Zika* 16258 (WTU); King Co., wet thicket, Madrona Park, W shore of Lake Washington, Madrona, Seattle, elev. 5 m, 2 Aug 2000, *Zika* 15184 (WTU).

*Previous knowledge.* Green ash is native to eastern North America, west to Montana, and planted as an ornamental in the Pacific Northwest.

*Significance.* First record for Washington escaping from cultivation and naturalizing.

*GALIUM PEDMONTANUM* (Bellardi) All. (RUBIACEAE).—Klickitat Co., disturbed meadow, Conboy National Wildlife Refuge, elev. 570 m, 15 Jun 2001, *Rodman* 508 et al. (WTU).

*Significance.* First report for Washington for this European native.

*GERANIUM PYRENAICUM* Burm. f. (GERANIACEAE).—King Co., gravel alleys and waste ground, Madrona, Seattle, elev. 95 m, 14 May 2000, *Zika* 14969 (OSC, WS, WTU).

*Previous knowledge.* Hedgerow cranesbill is native to Europe, grown in gardens, and known as a weed in California and eastern North America.

*Significance.* First report in Washington as an escape from cultivation.

*HIERACIUM LACHENALII* C.C. Gmel. (ASTERACEAE).—King Co., sunny roadside, Route 410, Greenwater, 14 Jun 2001, *Walker* s.n. (WTU); Skamania Co., north ridge of Table Mountain, 25 Jun 2000, *Arnett* s.n. (WTU); Snohomish Co., logged area, Perry Creek trail, 5 Aug 1962, *Kruckeberg* 5515 (WTU); common on roadside, Route 2 east of Index, elev. 300 m, 5 Jun 2000, *Zika* 15095d (WTU).

*Previous knowledge.* *Hieracium lachenalii* s. str. (syn. *H. acuminatum* Jord.) is native to Europe and adventive

in eastern North America. All reports of *H. vulgatum* Fries from Washington are *H. lachenalii*, except one collection of true *H. vulgatum* from Pacific Co. (*Maxwell* 215 WTU).

*Significance.* First collections for Washington.

*HIERACIUM MURORUM* L. (ASTERACEAE).—Pierce Co., roadside and adjacent forest, Route 706 at Westside Road, Mt. Rainier National Park, elev. 640 m, 14 Aug 1999, *Biek* 2 (WTU).

*Previous knowledge.* Wall hawkweed is native to Europe, and adventive in eastern North America. Reports of *H. atratum* Fries from Washington belong here. *Hieracium murorum* has been collected as a weed in Portland, Oregon (*Ornduff* 6196 OSC, WTU).

*Significance.* First collection for Washington.

*HIERACIUM SABAUDUM* L. (ASTERACEAE).—King Co., roadside, Interstate 90, 16 km E of North Bend, elev. 420 m, 20 Sep 2001, *Brunskill* s.n. (WTU); Skagit Co., roadside, Cain Lake Road near Alger, 3 Sep 1996, *Lantz* s.n. (WTU); Whatcom Co., E Lake Samish Road, ca. 10 km S of Bellingham, 2 Sep 1990, *Burnett* 280 (WTU); Interstate-5, near S end of Samish Lake, elev. 30 m, 9 Sep 2000, *Zika* 15465 (WTU).

*Previous knowledge.* Savoy hawkweed is native to Europe and adventive in eastern North America and British Columbia. Reports of *H. laevigatum* Willd. from Washington belong here.

*Significance.* First report for Washington.

*HYPERICUM MACULATUM* Crantz subsp. *OBTUSIUSCULUM* (Tourlet) Hayek (CLUSIACEAE).—King Co., crack in concrete sidewalk, Montlake, Seattle, elev. 25 m, 22 Jul 2001, *Zika* 16393 (WTU).

*Previous knowledge.* Dotted St. Johnswort is native to Europe, and adventive in southern British Columbia. In Seattle it is spreading from an introduction in a "wildflower" seed mix.

*Significance.* First report for Washington.

*JUNCUS PATENS* E. Mey. (JUNCACEAE).—Clark Co., shade of *Fraxinus*, Lackamas Creek floodplain, elev. ca. 65 m, 22 Mar 2001, *Zika* 15799 (WTU); low ground near SE 1st Street, Grass Valley, elev. ca. 70 m, 22 Mar 2001, *Zika* 15802 (WTU).

*Previous knowledge.* Native in the Willamette Valley of Oregon, 20 km to the S. "Reported but not seen from Washington" (Hitchcock, Cronquist, and Ownbey, 1969, *Vascular Plants of the Pacific Northwest*, Part 1, Univ. of Washington Press).

*Significance.* First collections to document this native in Washington.

*MOENCHIA ERECTA* (L.) P. Gaertn., B. Mey. & Scherb. (CARYOPHYLLACEAE).—Pierce Co., dry prairie remnant, with *Lepidium heterophyllum*, N of Muck Creek, elev. ca. 120 m, 4 Jun 2001, *Zika* 16157 & Weinmann (WTU); dry prairie remnant, Route 507, 5 miles NE of Roy, elev. ca. 120 m, 4 Jun 2001, *Zika* 16166 & Weinmann (WTU).

*Previous knowledge.* Upright chickweed is native to Europe, and adventive in Oregon and British Columbia.

*Significance.* First report for Washington.

*PHOTINIA DAVIDIANA* (Decne.) Cardot (ROSACEAE).—King Co., bird-sown epiphyte in tree, near Lake Washington, Martha Washington Park, Seattle, elev. 10 m, 6 Jun 2001, *Zika* 16184 & Jacobson (UBC, WTU); Kitsap Co.,

with *Alnus rubra*, pondshore, Bloedell Reserve, N end of Bainbridge Island, Puget Sound, elev. 30 m, 15 Nov 1999, *Zika 14724 & Jacobson* (WTU).

*Significance.* First collections of garden escapes for this native of China.

*PHOTINIA VILLOSA* (Thunb.) DC. (ROSACEAE).—King Co., moist ground, with *Alnus rubra*, *Rubus spectabilis*, Union Bay, Seattle, elev. 5 m, 29 Sep 2000, *Zika 15524* (WTU); rare adventive, Volunteer Park, Seattle, elev. 130 m, 8 Nov 2000, *Zika 15670 & Jacobson* (WTU).

*Previous knowledge.* Oriental redbud is native to E Asia, and known as a garden escape in the eastern United States. Both King Co. sites are adjacent to ornamental plantings, and the species was apparently spread by frugivorous birds.

*Significance.* First report from Washington as an escape from cultivation.

*PYRACANTHA COCCINEA* M. Roem. (ROSACEAE).—King

Co., near shore of Portage Bay, Seattle, elev. 5 m, 27 Aug 1999, *Zika 14136 & Jacobson* (WTU); San Juan Co., 3.5 km SE of Sportsman Lake, San Juan Island, 24 Oct 1999, *Zika 14641* (WTU).

*Significance.* First Washington report as an escape from cultivation.

*STACHYS ARVENSIS* (L.) L. (LAMIACEAE).—King Co., weed on gravel roadside, near S shore of Steele Lake, Federal Way, 3 Apr 2001, *Zika 15866* (WTU).

*Significance.* First collection in Washington for this European native.

*VERONICA VERNA* L. (SCROPHULARIACEAE).—Asotin Co., Route 129, Buford Cr., elev. 600 m, 30 May 1991, *Zika 11135* (OSC, WTU, WS); Chelan Co., N shore Lake Chelan, elev. 335 m, 7 Jun 1998, *Zika 13427* (WTU).

*Significance.* First report for Washington.

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## REVIEW

*A cactus odyssey: journeys in the wilds of Bolivia, Argentina, and Peru.* By JAMES D. MAUSETH, ROBERTO KIESLING, AND CARLOS OSTOLAZA. 2002. Timber Press, Portland, OR. 306 pp. ISBN 0-88192-526-8.

This wonderful book presents an engrossing account of the authors' botanical fieldwork in all manner of habitats throughout much of South America over a seven-year period. The relaxed narrative style, beautiful photographs, and liberal interjection of humor make this an entertaining read for just about anyone. Indeed, approachability by the layperson is a stated goal of the work, and one that is met very admirably. For botanists, the book will be even more absorbing, as intriguing aspects of taxonomy, morphology, anatomy, ecology and physiology of cacti are highlighted throughout. As a cactus freak, I found the work completely enthralling.

I am very inspired by the authors' philosophy, stated clearly at the beginning and throughout the work: that cooperation, openness and sharing of findings among biologists is beneficial to all. It is quite refreshing to view this opinion in print. The fruits of this philosophy are evident in the quality and number of publications resulting from the fieldwork documented here (Kielsing 1995; Mauseth and Kielsing 1997; Ostolaza 1997; Mauseth 1999, 2000; among others).

Seven chapters are included: one on cactus biology, and two each on the fieldwork conducted in Bolivia, Peru, and Argentina, respectively. The introduction to cacti is broadly written and accessible, resulting in a concise yet thoughtful description of the family, its evolution, ecology, and taxonomy. My one minor criticism of the book is in this introduction, where the movement of an ocean current is described somewhat inaccurately (p. 22). The circumglobal southern ocean current (Bartholomew 1958, Plate 2) precludes movement of water from the Atlantic to the Pacific between South America and Antarctica. This is the most minor of criticisms, however.

Subsequent chapters entwine absorbing vignettes of all manner of cacti in a chronological framework of field experience. The discovery of each new taxon on the journey is used to highlight one or more interesting facets of cactus biology. For example, the appearance of *Melocactus* includes a discussion of cephalia, or the sight of *Prosopis* (Fabaceae) and *Prosopanche* (Hydnoraceae) touches off a discussion of mistletoes found in cacti. The authors consistently relate the spotlighted theme for that taxon

to other plants, often drawing parallels between the plants encountered and other cacti more familiar to the North American reader. The authors have done a tremendous job here; I cannot emphasize enough how captivating and diverse a portrait of cacti is presented in this way. The biological material presented is written accessibly, but without apparent oversimplification. I also appreciate the time spent describing those aspects of cactus biology that are not easily understood. The authors' repeated appeals for students to study these phenomena are a welcome incorporation in the work.

Equally appealing is the description of the vagaries of the field. The less-than-ideal road conditions, rough accommodations, cold food, unsympathetic authorities and vehicle breakdowns of fieldwork are related with the dry wit that I have associated with Mauseth since taking his plant anatomy course in 1997. Here, his sense of humor is unerring. Anyone who has spent time afield will find themselves at least smiling but probably laughing outright at the dead-to-rights depiction of being constantly outpaced by the sun.

The photographs are all excellent, and well chosen to illustrate particular points. South America is a beautiful, wild, diverse place as pictured here, and the cacti are flat-out gorgeous. My own favorites include figures of *Browningia candelaris* and *Azuroocereus*. Many wonderful landscape and habitat shots are included, as well as several graphical depictions of life in the field.

This book has something for everyone, and I recommend it to all. I am in the middle of my second reading, and it has not lost an ounce of my interest.

—M. PATRICK GRIFFITH, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711. E-mail: michael.patrick.griffith@cgu.edu.

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## ANNOUNCEMENT

### BIENNIAL GRADUATE STUDENT MEETING AND ANNUAL BANQUET

15 FEBRUARY 2003 AT THE UNIVERSITY OF  
SAN DIEGO

The California Botanical Society's Biennial Graduate Student Meeting and Annual Banquet will be held on Saturday, 15 February 2003 at the Hahn University Center of the University of San Diego. Graduate students everywhere who are initiating, conducting, or finishing research projects in any area of botany (e.g., ecology, evolution, conservation, floristics, morphology, development, etc.) are encouraged to attend the meeting (and banquet) and to give short oral presentations on their research plans or findings. The venue is an ideal opportunity for students to gain experience giving presentations in the standard format of scientific meetings, to meet students involved in botanical research from other institutions, and to learn more about botany in general. Presentations will be judged by student peers and awards for best papers in proposed research, research-in-progress, and completed research will be presented at the evening banquet.

Abstracts of all presentations will be published online at the California Botanical Society web-site ([www.calbotsoc.org](http://www.calbotsoc.org)).

Our speaker for the annual banquet will be Dr. Jon Rebman, Curator of the Herbarium at the San Diego Natural History Museum, who will present an after-dinner lecture entitled "Discoveries on a Floristic Frontier: Baja California." Dr. Rebman's botanical explorations of remote regions of Baja California are exemplary of binational collaboration between the US and Mexico and have yielded many exciting findings, including plants previously unknown to science and new insights into cactus biology and evolution. We look forward to a fascinating evening of highlights from Dr. Rebman's field research in beautiful and rugged desert ranges, such as the Sierra de la Giganta, where he will be involved in a major expedition this fall.

The graduate student meeting and annual banquet are open to CBS members and non-members alike; anyone interested in the meeting and/or banquet is encouraged to attend. Registration information for the meeting and banquet will be forthcoming.

ERRATUM

STUTZ, H. C., M. R. STUTZ, AND S. C. SANDERSON. 2001. *Atriplex robusta* (Chenopodiaceae), a new perennial species from northwestern Utah. Madroño 48:112–115.

The name "*Atriplex robusta*" H. C. Stutz, M. R. Stutz, & S. C. Sanderson (Madroño 48:112. 2001) is illegitimate, having already been used (*A. robusta* Speg. In Gand.)

***Atriplex tridentata* Kuntze var. *robusta* H. C. Stutz, M. R. Stutz, & S. C. Sanderson, var. nov.**—TYPE: USA, Utah, Tooele Co., 1 mi W of Knolls, T15 R13W S15, shoulder of highway I-80, 1280 m elevation, 16 Sep 1977, *H. C. Stutz 8141* (Holotype: BRY; Isotypes, BRY, CA, CAS, GH, MO, NY, RM, UC).

Frutices caespitosi, 40–80 cm alti. Caules erecti vel ascendentes, ramosi a basi ad apicem, dense

furfuraceus, 1–8 mm diam., fragilis. Folia oblonga, ascendentia usque appressa, dense furfuraceae; folia ephemera verna et aestiva 15–30 mm longa, 5–10 mm lata; folia serotina aestiva et hiberna 3–10 mm longa, 2–5 mm lata, anatomia foliaris Kranz-typi. Plantae dioeciae, raro monoeciae. Flores staminati sessiles, ad brevi-ramulus axillares in angusti paniculas terminales; perianthium campanulatum, 5-partitum ad medium, dense furfuraceum, segmentis ovatis usque ellipticis, 2 mm longis, 1 mm latis; stamina 5, filamentis 1 mm longis, antheris ca. 2 mm longis, 1 mm latis. Flores pistillati solitarii, sessiles, in pleurumque sine foliis confertas paniculas terminales. Bractae fructiferae furfuraceae, compressae, urceolatae, latissimae infra media, 5 mm latae, 7–8 mm longae, exappendiculatae, cum 3–10 marginalibus dentibus, 0.5–2 mm longis, qui medianus longissimus. Utriculus orbiculatus, pericarpio membranceo pellucido. Semena 5 mm diam., testa membranacea, brunnea; radícula supra.

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FLOWERING PATTERNS AND REPRODUCTIVE ECOLOGY OF  
*MAMMILLARIA GRAHAMII* (CACTACEAE), A COMMON, SMALL CACTUS  
IN THE SONORAN DESERT

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ABSTRACT

*Mammillaria grahamii* is an outcrossing species that can flower as many as four times a year. The number of flowers produced by an individual plant depends largely on plant volume. Fruit set is high, about 77%. Flowers normally live one day but can open a second day when pollination is inadequate. Flower production within a population varies interannually and increases with rain in the week before flowering. Even heavy rains do not induce all potentially fertile tubercles to flower during a single event. Because some tubercles are withheld, plants can flower several times a year, given appropriate conditions. *Mammillaria grahamii* plants risk poor fruit set if they happen to flower when pollinator populations are low or when pollinators preferentially visit other species. Withholding of tubercles might allow plants to spread this risk across the entire flowering season, thus increasing the probability that flowering will coincide with pollinator activity.

Key Words: Cactaceae, floral biology, floral longevity, *Mammillaria grahamii*.

When and how often plants bloom has profound consequences for seed set, seed dispersal, and seedling recruitment, thus making the study of flowering phenology an important aspect of plant population biology (Primack 1985; Rathcke and Lacey 1985; Newstrom et al. 1994). Because flowering patterns affect the behavior and reproductive success of pollinators and granivores, phenology underlies the study of evolutionary and community ecology as well (Brody 1997). Knowledge of flowering patterns is, moreover, crucial to conservation and management of rare species (Newstrom et al. 1994). For example, *Coryphantha robustispina* (Schott ex Engelm.) Britton & Rose subsp. *scheeri* (Muehlenpfordt) N. P. Taylor, a small, endangered cactus, can bloom several times per year, but because the proportion of sexually mature plants that flower during any single event varies considerably (Roller 1996), within-year flowering patterns must be considered when estimating reproductive effort.

In general, flowering patterns and reproductive biology of small cacti in the arid southwestern United States are poorly known (Johnson 1992). The few species that have been studied are for the most part endangered or threatened, giving us a poor idea of what phenological and floral traits are associated with successful reproduction and establishment. This paper examines the reproductive ecology of *Mammillaria grahamii* Engelm., a small cactus that is common and widespread in and around the Sonoran Desert (Shreve and Wiggins 1964; Aguilar et al. 2000). The species has been known as *M. microcarpa* Engelm., not a validly published name (Aguilar et al. 2000).

The reproductive ecology of *M. grahamii* has not

been studied in any detail. Flowers are bowl-shaped and are relatively small for the family, about 2 to 4 cm in diameter (Anderson 2001). They arise from areoles located in the axils of old tubercles, that is, tubercles formed the previous year or earlier (Shreve and Wiggins 1964). Tubercles are modified leaf bases that appear as regularly spaced projections on the plant body. Once an areole has flowered, it cannot flower again (Gibson and Nobel 1986). Petals are deep pink or white with a pink midrib. Size, shape, and diurnal habit of the flowers indicate that they are bee-pollinated (Grant and Grant 1979). Stems are solitary or branching and grow to a height of 10 to 20 cm. Maximum lifespan is about 11 years (Goldberg and Turner 1986).

*Mammillaria grahamii* can flower several times per year and in any month from March to September (personal observation; M. Dimmitt personal communication). The ultimate goal of this study was to determine the benefits of multiple flowering events and the conditions under which they occur. Specific objectives were to determine: 1) relation between plant size and flower production, 2) effect of rain on flower production, 3) longevity of individual flowers, 4) minimum reproductive size, 5) breeding system, and 6) fruit set and seed production.

METHODS

*Study area.* The study site is located at 720 m above sea level about 11 km northwest of Tucson, Pima County, Arizona (32°16'N, 111°2'W). Terrain is a level to gently sloping alluvial terrace. Soils are derived from rhyolitic parent material, and the surface is gravelly to cobbly. Vegetation is characteristic of the Arizona Upland subdivision of the

Sonoran Desert (Shreve and Wiggins 1964). Dominant plants include *Cercidium microphyllum* (Torr.) Rose & Johnston, *Ambrosia deltoidea* (A. Gray) Payne, *Acacia constricta* Benth., *Larrea tridentata* (Moc. & Ses.) Cav., *Krameria grayi* Rose & Painter, *Carnegiea gigantea* (Engelmann) Britton & Rose, *Opuntia engelmannii* Salm-Dyck., *Ferocactus wislizeni* (Engelmann) Britton & Rose and *Opuntia leptocaulis* DC. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter and early spring (November to March), an arid late spring (April to June), a predictable summer monsoon (July to August), and a highly variable autumn (September to October). Maximum temperatures in summer often exceed 40°C. Minimum temperatures rarely drop below -6°C in winter. Although freezing nights can be frequent in winter, daytime temperatures always rise above 0°C.

**Flower production and plant size.** On July 24, 1996, height and diameter of all stems on 60 *M. grahamii* plants were measured to the nearest 0.5 cm, and the number of flowers and flower buds on each stem was counted. Plants too small to flower were excluded from the sample. Stem volume was approximated using the formula for a cylinder, then individual volumes were summed to get volume of the entire plant. Number of flowers was used as the dependent variable in separate linear regressions against height of the tallest stem, diameter of the thickest stem, number of stems, and plant volume.

**Annual flowering patterns.** For monitoring frequency, duration, and intensity of bloom, all *M. grahamii* plants ( $n = 68$ ) within an area approximately 15 m by 20 m were marked on July 27, 1996 by affixing numbered aluminum tags to the ground next to the plant. The sample included some but not all of the plants sampled previously and also included plants that were too small to flower. Height and diameter of the tallest stem of each plant were measured to the nearest 0.5 cm. The number of open flowers on each plant in the sample was counted daily from the first to the last day of bloom whenever the sample flowered in 1996 (with one exception, described below) and 1997. In addition, open and spent flowers were counted on the last day of a single blooming event in 1999. Daily values in 1996 and 1997 were summed to determine the total number of flowers produced per plant during each event. Flower production during the first blooming event of 1996 was determined on the last day of the event by counting number of open and spent flowers. At the first event in 1996, flowers were counted on 25 single-stemmed plants only. Thereafter, all marked plants were sampled at every event.

**Rain and flower production.** The effect of rain on flower production was assessed for six flowering events in 1996, 1997, and 1999 using only those plants for which flowers had been counted at all six

events ( $n = 15$  plants). The mean number of flowers per plant at each event was calculated, then Spearman rank-order correlation was used to determine the strength of association between flower production and rain (mm) in the weeks before flowering.

**Pollinator visitation.** Visits by potential pollinators were monitored from August 3 to 6, 1996. Altogether, 25 flowers on 14 plants were watched for 10 minutes each, during which time the number of bee visitors was recorded. No attempt was made to identify the bees. Beetles, which are not effective pollinators of cactus flowers (Grant and Connell 1979), were not included in these surveys. Observations were made between 0830 and 1130 hr, the period of greatest pollinator activity.

**Characteristics of fruits and seeds.** Twenty-four ripe fruits were collected in September 1996 and individually weighed to the nearest 0.001 g. Length and width of each fruit were measured to the nearest 0.5 mm. Seeds were removed and air-dried, then the mass of seeds from each fruit was measured to the nearest 0.001 g. Seed set was determined by counting the number of seeds in each fruit. The weight of an individual seed was calculated by dividing seed mass by number of seeds.

**Fruit set.** Fruit set, defined as the proportion of flowers that produced fruits, was studied during two separate blooming events in August 1997. Thirty reproductively mature plants, none included in the previous samples, were numbered and tagged. Fifteen were randomly selected and covered by wire mesh cages to prevent pollinators from getting access to the flowers. The number of set fruits was counted several weeks after flowering ended. Separate Mann-Whitney tests were used to determine the effect of treatment (caged or open-pollinated) and blooming event (first or second) on the proportion of flowers that set fruit.

**Flower longevity.** The lifespan of individual flowers was studied on the same sample of 30 plants during the first summer blooming event in August 1997. All flowers opening for the first time were marked on a daily basis with glass-headed pins, using a different color of pin for each day. The number of freshly opened flowers and the number that opened more than once were counted on each plant every day.

**Breeding system.** Pollination and germination experiments in a greenhouse were used to determine the breeding system. Altogether, 10 self pollinations (two flowers from the same plant) and 6 cross pollinations (two flowers from different plants) were made. For each cross, one of the flowers was tagged with a label indicating date and cross number. Stamens were removed from both flowers, then the stamens of the untagged flower were used to pollinate the stigmas of the tagged flower. Tagged



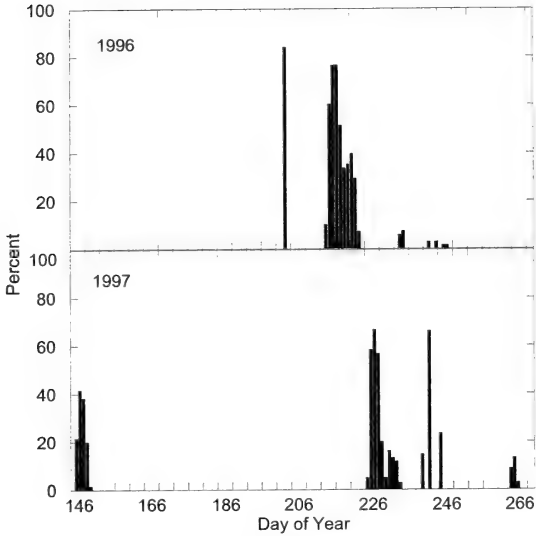


FIG. 1. Flowering curves for *Mammillaria grahamii* in 1996 (top) and 1997 (bottom). Y axis represents percent of sample in flower; n = 68 except for first event of 1996, where n = 25. The first event in 1996 lasted five days but flowers were counted only on the final day.

flowers were checked regularly for developing fruits. Mature fruits were collected and dried, and the number of seeds in each was counted.

Seed germination was tested using fruits from cross and self pollinations. Twenty seeds from each fruit were planted in a four-inch-square plastic pot on a moistened, sterilized mixture of sand, turface, and milled peat moss. The pots were covered with clear plastic wrap to prevent desiccation while allowing exposure to light. After two months, the covers were removed and the pots watered weekly during the next three months, then every two weeks for the following seven months. The number of living and dead seedlings in each pot were counted at two months and twelve months.

RESULTS

*Annual flowering patterns.* As reported previously, *M. grahamii* can flower three to four times in a year (Fig. 1). Flower dates in this study were as follows: July 21 to 25, 1996; August 2 to 11, 1996; May 26 to 30, 1997; August 14 to 20, 1997; August 29 to September 3, 1997; and September 21 to 23, 1997. In both years, the most intense blooming events occurred in summer and lasted more than a week (Fig. 1). Typically, 60 to 80% of the sample flowered during the first summer event. Later summer events involved fewer plants and lasted only three to four days. No flowers were produced in spring of 1996. Spring flowering in 1997 involved about 40% of the population and lasted five days.

*Flower production and plant size.* In the sample of reproductively mature plants (n = 60), volume

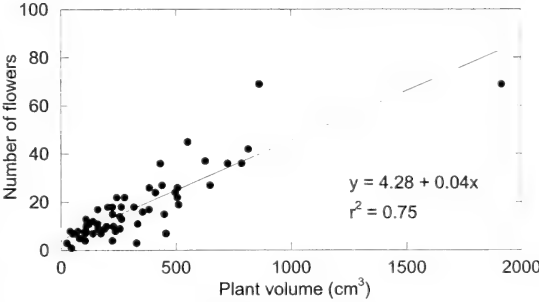


FIG. 2. Flower production in a single flowering event as a function of plant volume (n = 60).

explained 75% of the variation in flower number (P = 0.001) (Fig. 2). Number of stems and height of the tallest stem respectively accounted for only 44% (P = 0.001) and 32% (P = 0.001) of the variation in number of flowers. Diameter of the thickest stem was not significantly correlated with flower production ( $r^2 = 0.06$ , P = 0.07). In the 68-plant sample, which included plants too small to flower, the smallest plants to bloom were 2.5 cm in height; virtually all plants > 4 cm in height produced flowers.

*Rain and flower production.* Spearman correlation analysis showed that rain in the week before flowering was strongly correlated with mean number of flowers produced by 15 plants during six flowering events ( $r_s = 0.94$ , P < 0.05) (Fig. 3).

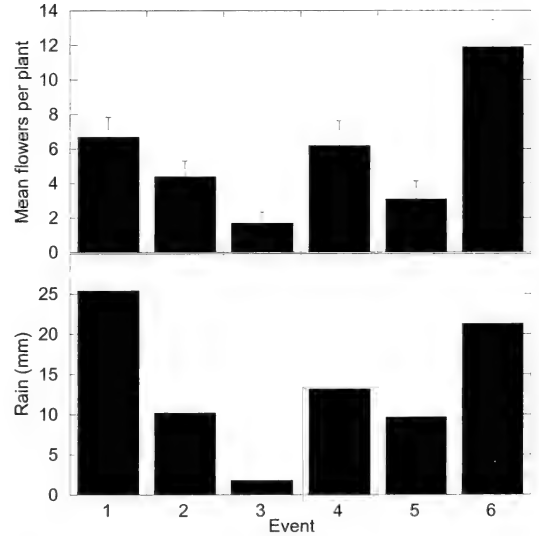


FIG. 3. Correlation between flower production and rainfall. Top: mean number of flowers/plant ( $\pm 1$  SE) at six flowering events. Bottom: rain (mm) in the week before flowering. First day of flowering as follows: event 1, August 2, 1996; event 2, August 21, 1996; event 3, May 27, 1997; event 4, August 15, 1997; event 5, August 29, 1997; event 6, July 14, 1999.

TABLE 1. FRUIT AND SEED CHARACTERISTICS, *MAMMILLARIA GRAHAMII*; PEARSON CORRELATION COEFFICIENTS (N = 24 FRUITS). \* = Significant at  $P < 0.001$ .

	Fruit mass	Fruit length	Fruit width	Seed mass
Fruit length	0.54			
Fruit width	0.75*	0.13		
Seed mass	0.40	-0.32	0.75*	
Seed number	0.45	-0.25	0.73*	0.89*

Mean flower production was also correlated with rain in the two weeks before flowering ( $r_s = 0.90$ ,  $P < 0.05$ ) but not with rain in the three weeks before flowering ( $r_s = 0.77$ ,  $P > 0.05$ ).

**Pollinator visitation.** Visitation varied considerably over four days: visits/flower/hr ( $\pm$ SD) on the first through fourth days of observation were 0.0,  $5.3 \pm 3.6$ ,  $5.0 \pm 2.4$ , and  $41.1 \pm 25.3$ , respectively. Cloudy, humid weather on the first day of observation may have limited pollinator activity; the remaining days were clear and hot. On the second and third days of observation, all flower visitors were small bees, whereas on the fourth day, most visitors were honeybees.

**Characteristics of fruits and seeds.** In the wild population, the number of seeds per fruit averaged  $149 \pm 45$  (SD). Fruit length and width ( $\pm$ SD) were, respectively,  $26.0 \text{ mm} \pm 5.2 \text{ mm}$  and  $7.2 \text{ mm} \pm 0.9 \text{ mm}$ . Mass of all seeds in a single fruit averaged  $0.038 \text{ g} \pm 0.016 \text{ g}$  (SD). Calculated mass of an individual seed was 0.0003 g. Seed mass constituted on average 9.1% of fresh fruit mass. Fruit width was the best predictor of number of seeds, seed mass, and fruit mass (Table 1). In addition, seed mass and number of seeds were highly correlated (Table 1).

**Fruit set.** Fruit set of caged and open-pollinated plants averaged, respectively, 1.4% and 68.0% in the first blooming event, 1.1% and 85.0% in the second. The difference between treatments was highly significant (Mann-Whitney  $U = 0.0$ ,  $P = 0.001$ ), but the difference between blooming events was not (Mann-Whitney  $U = 350.0$ ,  $P = 0.70$ ).

**Flower longevity.** Most flowers, whether caged or not, opened only a single day. Nevertheless, the proportion of flowers that opened a second day was almost 14 times greater for caged (63 of 284 flowers) than uncaged plants (3 of 188 flowers). It appears that flowers typically live a single day if the level of pollination is adequate and that they can sometimes open a second day if it is not.

**Breeding system.** Fruit set was 100% for crossed flowers (6 of 6) but only 10% for selfed flowers (1 of 10). The single fruit produced from the self-pollinated flowers contained 281 seeds, but none germinated. Thus, in the rare instance when self pollination yielded fruit, the seeds apparently were not

viable. The average number of seeds in fruits produced by cross pollination was  $208 \pm 45$  (SD). This was considerably higher than in the wild population and probably reflects a difference in pollen loads. Seeds from cross-pollinated fruits were highly germinable. Two months after planting, germination averaged 11.7%. After twelve months, average germination was 78.3%.

## DISCUSSION

In some respects, the floral biology of *M. grahamii* is similar to that of other small cacti in the arid southwestern United States (Table 2). As for *Echinomastus erectocentrus* (J. M. Coulter) Britton & Rose (Johnson 1992) and *Escobaria robbinsorum* (W. H. Earle) D. R. Hunt (Schmalzel et al. 1995), plants reach reproductive maturity at a small size, and flower production increases as plants grow. As with *Scleroactus polyancistrus* (Engelmann & Bigelow) Britton & Rose (May 1994), variability in flower production from year to year or event to event is strongly correlated with rain.

In other respects, the reproductive strategy of *M. grahamii*, a common and relatively widespread species, differs from that of small cacti that are rare or narrowly distributed. The number of flowers per plant and seeds per fruit is considerably higher (Table 2). The potential flowering season is longer, as well, and there can be two to four times as many flowering events per year (Table 2), a pattern that Newstrom et al. (1994) describe as "subannual." The abundance and distribution of any species necessarily arises from multiple intrinsic, environmental, and historical factors and cannot be ascribed to reproductive biology alone. Nevertheless, the combination of subannual blooming, large number of flowers per plant, high fruit set, and high seed production makes *M. grahamii* substantially more fecund than other small cacti (Table 2) and doubtless contributes to its success.

Small cacti are at high risk of illicit collection (Bennett et al. 1986). During one study, for example, collectors illegally removed 31% of 324 *M. grahamii* and 44% of 9 *M. thornberi* Orcutt (Bennett et al. 1986). The latter species is considered vulnerable (Nabhan et al. 1989). Although the percentages are roughly equivalent, the number of plants remaining—23 versus 5—is not. Especially for small cacti that have low fecundity, such depredations can represent a substantial portion of the reproductive capacity of the population.

It remains to be seen whether *M. grahamii*, like other small cacti in the region, is obligately outcrossing. In greenhouse experiments, only 1 of 10 self-pollinated flowers set fruit. Because these flowers received ample pollen, low fruit set was likely a consequence of self incompatibility rather than inadequate transfer of pollen from stamens to stigmas. None of the seeds from the selfed fruit germinated, in contrast to seeds from cross-pollinated

TABLE 2. COMPARATIVE FLORAL BIOLOGY OF SELECTED SMALL CACTI. Species abbreviations and data sources as follows: CORY, *Coryphantha robustispina* subsp. *scheeri* (Roller 1996); ECHI, *Echinomastus erectocentrus* (Johnson 1992); ESCO, *Escobaria robbinsorum* (Schmalzel et al. 1995); MAMM, *Mammillaria grahamii*; SCLE, *Sclerocactus polyancistrus* (May 1994). Flower and stem sizes are from Anderson (2001). Other abbreviations: SS, single-stemmed; MS, multiple-stemmed; n.d., no data. Information on status is from <http://arizonaes.fws.gov> and <http://www.cnps.org>.

	CORY	ECHI	ESCO	MAMM	SCLE
Flower diameter	5–7	4–5	1–2	2–4	5
Stem height (cm)	5–15	10–37	2–6	7–20	10–40
Stem diameter (cm)	5–9	7–12	2–6	7–11	5–9
Flowers/plant/yr (range)	1–23	1–16	1–7	1–136	1–6
Flowers/plant/yr (mean)	7	n.d.	2	23	4
Height at first flowering (mm)	30	24	13	25	30
Breeding system	Outcrossing	Outcrossing	Outcrossing	Outcrossing	Outcrossing
Fruit set (percent)	71	94	93	77	n.d.
Seeds/fruit	89	92	20	149–209	120
Germination (percent)	89	n.d.	n.d.	12–78	“low”
Flower longevity (days)	1	n.d.	n.d.	1 (2)	3?
Flowering season	May–Jul	Mar–Apr	Mar–Apr	Mar–Sep	Apr–May
Flowering events/yr	1–3	1	1	1–4	1
Duration of events (days)	1	27	n.d.	3–11	n.d.
Lifespan (yr)	<30	n.d.	17	11	17
Plant morphology	SS, MS	SS	SS	SS, MS	SS
Status	Endangered	Candidate	Threatened	Not listed	“Watch”

fruits, which germinated at a high rate. Taken together, the pollination and germination experiments suggest that *M. grahamii* is obligately outcrossing; additional experimental work is needed to determine whether this is indeed the case.

Because *M. grahamii* produces only a single flower in each axil, flower production in one year is ultimately limited by the number of tubercules produced in previous years and by the proportion of old tubercules that have already flowered. Annual tubercule production is in turn determined by plant volume and, probably, rainfall. The intensity of bloom during any single event is also a function of rain, at least in part. When rains are minimally adequate, the proportion of tubercules that flower is small; when rains are relatively large, many tubercules bloom (Fig. 3). On the other hand, even heavy rains do not induce all potentially fertile tubercules to flower during a single event. Because some tubercules are withheld, plants can flower several times a year, given appropriate conditions.

Fruit set of *M. grahamii* and certain other small cacti is relatively high (Table 2). In the case of *Echinomastus*, fruit set apparently is not affected by pollinator abundance or effectiveness (Johnson 1992). This might not be true for *M. grahamii*. The results of the caging experiment suggest that plants risk poor fruit set if they happen to flower when pollinator populations are low or when pollinators preferentially visit other species. This does happen at least occasionally, as in 1996 when visitation on one day was essentially nil. Withholding of tubercules might allow plants to spread the risk across the entire flowering season, thus increasing the probability that flowering will coincide with pollinator activity.

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THE EFFECT OF FIRE AND COLD TREATMENTS ON SEED  
GERMINATION OF ANNUAL AND PERENNIAL POPULATIONS OF  
*ESCHSCHOLZIA CALIFORNICA* (PAPAVERACEAE) IN  
SOUTHERN CALIFORNIA

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ABSTRACT

Throughout its native range, the California poppy, *Eschscholzia californica*, exhibits substantial morphological and life-history variation, including variation in seed dormancy and ability to perennate. Populations from xeric southern California habitats have high seed dormancy over a range of habitats that span from coast to desert and across vegetation types of varying fire frequency. Understanding variation in the cues that break dormancy in this species is especially important to managing natural populations with prescribed fire, and in production and use of local ecotypes for restoration, erosion control, and ecological landscaping. We explored the influence of sequential treatments of low temperature and components of fire (heat, dry smoke, smoke water, a commercially concentrated smoke water we call “liquid smoke”, charrate, and nitrate) on seed germination for both annual and perennial populations and compared results to those of widely used domesticated seeds. We also examined the effect of light and seed age. Domesticated seeds had no seed dormancy and, except for heat-treated seeds, germination was close to 100% across treatments, including water controls. In contrast, seeds of all wild southern California populations showed some dormancy, germination was highly conditional on test factors, and light inhibited germination. We found differences in dormancy rates among wild populations and years since seed collection, with annuals having higher dormancy than perennials in the first year following collection but not after aging > two years. Of the fire treatments, heat (85°C for 10 min), or heat plus smoke, resulted in significantly reduced germination and viability of all populations tested, including domesticated seeds. All smoke treatments significantly improved germination of dormant-seeded populations over water controls, but neither nitrate, water soaking, charrate, nor cold treatment alone broke dormancy. In the absence of cold treatment, both liquid and dry smoke yielded higher germination than controls in seeds aged 8–10 months (65–95% for liquid smoke, 21–60% for dry smoke, vs. 14–59% for controls). Moist cold treatment (3–9°C) by itself did not usually break seed dormancy but it did act synergistically to increase germination of smoke-treated seeds and did not harm controls. In contrast, for most populations colder pretreatment (~2°C) resulted in a small decrease in germination of water controls but not in seeds smoke-treated before cold treatment. Seed age affected germination of controls and the ability of smoke to break dormancy. Germination of controls and smoke-treated seeds increased between 2 and 4 mo of aging in the lab, with no further increase at 8 mo. Dormancy of controls was substantially higher in seeds aged in the lab > 27 months from collection relative to seeds aged 8–10 months ( $n = 7$  and 5 populations, means = 92% and 63% dormant, respectively). Smoke succeeded in breaking dormancy of older seeds to half the extent as in younger seeds, suggesting either a decline in germinability as seeds degrade, induction of a deep secondary dormancy, or both. Given the large differences between domesticated and wild populations in dormancy and germination requirements, and that seed dormancy is probably heritable and adaptive, non-dormant domesticated seeds are not appropriate for restoration, especially in xeric environments that naturally support plants with dormant seeds.

Key Words: *Eschscholzia*, fire, germination treatments, life-history variation, restoration, seed dormancy, smoke, stratification.

As the use of native plants for revegetation and landscaping gains popularity, and as restoration projects become more prevalent and species-inclusive, understanding seed germination biology be-

comes essential from both basic and applied ecological perspectives. In warm and dry climates, native seeds can be difficult to germinate because of dormancy, and they often require very specific germination cues. As is the case with many traits, both dormancy and response to dormancy-breaking signals can be locally adaptive and can differ dramatically within species, especially when they exist in a wide variety of habitats (Cruden 1974; Capon et al. 1978; Keeley 1986; Meyer et al. 1990; Meyer and Monson 1992). If cues that break seed dormancy are identified, then practitioners can use the information to maximize germination of out-plant-

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ed seeds and of seeds used for agricultural increase, thus limiting selection against genes conferring dormancy. Seed increase encourages use of local seed sources for restoration, landscaping, and roadside erosion control, thereby minimizing mismatching of important adaptive traits to planting location. Mismatches can decrease project success and introduce maladapted genes into wild populations (Montalvo et al. 1997; Keller et al. 2000; Montalvo and Ellstrand 2000, 2001).

The effects of fire on germination response are so common that it is worthwhile to include fire treatments in studies of seed dormancy, especially for species with close relatives known to be fire followers. Seeds of many species in Mediterranean climates, where fire is common, germinate in response to different fire-related cues (Keeley and Keeley 1987; Keeley 1991; Roche et al. 1997a, b, 1998). Also, as prescribed burning becomes an increasingly important management tool, it is important to examine the effects of fire on seeds, and to determine if populations from different environments have different requirements and vulnerabilities.

We chose California poppy (*Eschscholzia californica* Cham.) as a model species for studying variation in seed dormancy and response to different germination cues. California poppy occupies many habitats throughout its native range from Baja California to southern Washington state, and is native to a diverse range of climates, edaphic environments, and plant communities that vary in fire frequency, from coastal sand dunes to inland deserts, including fire-prone coastal sage scrub, chaparral, and grasslands. Populations exhibit a wide spectrum of morphologies and life histories, varying in flower color, size, seed dormancy, and other attributes, and can be annual (semelparous), long-lived perennial (iteroparous), or a facultative annual (Cook 1962). In addition, this species has prominent economic importance as the California state flower and is frequently used in restoration and revegetation. Information about variation in its germination response to the effects of fire and other factors is essential for long-term success of projects that utilize prescribed burning for restoration, for commercial seed production, and for conservation practice.

In southern California, native poppies (both annuals and perennials) germinate during the rainy season in mid winter; plants flower in late winter to spring, and produce seeds in the spring (late April to early June), although some perennials can defer flowering to the second spring and produce seeds over a longer season. Seeds appear to remain dormant (or conditionally dormant) until the next winter rains, which prevents early germination after infrequent summer storms and subsequent death from desiccation in the hot, dry summer environment. Thus plants appear to fit the "winter annual and perennial" syndrome (Baskin and Baskin 1998,

p. 54–56), but it is unknown whether the seeds follow an annual cycle of summer dormancy followed by non-dormancy or conditional dormancy during the winter. Based on the small linear embryo of California poppy seeds, seeds have been assumed to have morphophysiological dormancy in which embryos complete their maturation after seed dispersal and an environmental cue is required to break physiological dormancy (Martin 1946; Baskin and Baskin 1998). It is unknown if embryo growth and dormancy break require the same or different conditions.

In interior shrub- and grassland habitats of southern California, prolific displays of poppies in the absence of fire are periodic and tend to be separated by many years. In some years, flowering of annual populations is absent or scant and can be followed by boom years, demonstrating the existence of a substantial seed bank. This suggests that seeds may cycle through dormancy and conditional dormancy depending on environmental conditions. In addition, the conspicuous presence of poppies on recent burns when blooming is poor elsewhere (A. Montalvo personal observation, G. Hund, R. Noll, J. Crossman personal communication) suggests that, at least in these habitats, seeds survive fire and some component of fire aids in breaking seed dormancy.

In California, fire and fire components have been shown to break seed dormancy in many "fire-following" species, especially in sage scrub and chaparral communities (Keeley 1991). For example, seed dormancy of *Emmenanthe penduliflora* Benth., *Salvia columbariae* Benth., *S. mellifera* Greene, *Phacelia grandiflora* (Benth.) Gray, *P. minor* (Harv.) Thell., and *Lotus scoparius* (Nutt.) Ottley is broken by heat, smoke, or other components of fire (Keeley 1991; Keeley and Fotheringham 1998a, b). Each of these species occurs in a number of different plant communities, frequently concomitant with California poppy (Munz and Keck 1968). In studies of intraspecific germination response to heat, very different patterns were found among populations of perennial *S. mellifera* (Keeley 1986) and annual *S. columbariae* (Capon et al. 1978) from desert habitats vs. chaparral and coastal sage scrub. Given that the distribution of California poppy is even more diverse than for these *Salvia* species, its germination response to fire is likely at least as complex. The response of poppy seed germination to components of fire has not been studied, although prescribed burning is being used to manage portions of its native habitat, including the Antelope Valley California Poppy Reserve (AVCPR, [www.calparks Mojave.com/poppy](http://www.calparks Mojave.com/poppy); [www.parks.ca.gov/parkindex](http://www.parks.ca.gov/parkindex), J. Crossman, personal communication).

Data on the general germination biology of California poppy are scant, and few authors have identified use of wild rather than domestic seeds in their work (e.g., Cook 1961, 1962; Fox et al. 1995). Cook (1961, 1962) documented geographic varia-

TABLE 1. SEED POPULATIONS USED IN SEED GERMINATION EXPERIMENTS. Abbreviations: Pop = population; A = annual; P = perennial. Source, locality, and life-history strategy are listed for each study population.

Pop Code	Life history	Collection locality	Source of seeds and collection date
LC98	P	Antelope Valley area, <b>Lancaster</b> , CA	S&S Seeds (Carpinteria, CA) Lot #T8979, ~May 1998
AV00	P	<b>Antelope Valley</b> area 2, CA	L. Feist, May 25, 2000
Dom	P	Cultivar <b>domesticated</b> in Salem, OR 25–30 generations (origin s. California)	Stover Seed Co. (Los Angeles, CA), harvested for 2000 market
PR95	A	California State Parks, Antelope Valley California <b>Poppy Reserve</b> , CA (AVCPR)	J. Crossman, May 1995
PR96	A	as in PR95	G. Fox, ~May 1996
PR00	A	as in PR95	L. Feist, May 17, 2000
PR01	A	as in PR95	A. Montalvo and L. Feist, May 27, 2001
CB97	A	<b>Carlsbad</b> , CA	S&S Seeds (Carpinteria, CA), Lot #S7383, ~May 1997
NH98	A	<b>North Hills</b> of Western Riverside County Multi-Species Reserve, CA	R. Noll, S&S Seeds (Carpinteria, CA), Lot #T1008, Apr. 29–May 11, 1998
NH00	A	as in NH98	L. Feist, May 11–23, 2000
NH01	A	as in NH98	A. Montalvo, L. Feist, May 8–13, 2001
FM96	P	<b>Fairmont Butte</b> (s. of AVCPR)	G. Fox, ~May 1996
FM00	P	as in FM96	L. Feist, May 25 and June 6, 2000
FM01	P	as in FM96	A. Montalvo and L. Feist, May 27, 2001
EM98	A	Vicinity of <b>Estelle Mt.</b> , ne Lake Elsinore, Riverside Co., CA	R. Noll, S&S Seeds (Carpinteria, CA), Lot #T1022, May 7–9, 1998
EM00	A	as in EM98	R. Noll, S&S Seeds (Carpinteria, CA), Lot #V1022, May 8–11, 2000
SR101	P	Serpentine site, <b>Sedgwick Ranch</b> Reserve, Santa Barbara Co., CA	A. Montalvo and J. Skillman, May 19, 2001
RV01	P	<b>Riverside</b> , Riverside Co., CA, domesticated population	A. Montalvo May 27, 2001

tion in seed dormancy that was loosely correlated with habitat and longevity; annual and perennial populations from xeric sites had mostly dormant seeds, whereas perennial populations from mesic sites had little to no dormancy. He found that dormancy could sometimes be broken with gibberellic acid (GA3), but he did not identify the natural cues that break dormancy.

Here we assessed the germination response of *E. californica* seeds from several southern California populations to various components of fire and other potential dormancy breaking conditions. We included seeds from both annual and perennial wild populations, neighboring and distant populations, and a variety of climate regions including coastal, inland, and desert. We examined whether the populations varied in seed dormancy, effect of seed aging, and in germination response to a variety of fire treatments, including heat, smoke, charrate, and nitrogen. Poppies do not usually germinate until well into the cold season (December–February). Because many GA3 responsive seeds also respond to cold treatment, we also explored the effect on germination of exposure to a short period of cold temperatures (e.g., Roche et al. 1998), using varying temperatures, length of exposure to cold, and moisture levels during exposure to cold.

METHODS

*Study populations.* All wild populations were from southern California and represented both annual and perennial life-histories (Table 1). Seed collection codes designate site of collection followed by year of collection (i.e., 97 for 1997; 00 for 2000 and so on). Seeds were collected usually in May just before capsules exploded. Habitats of wild source populations varied as to vegetation type, precipitation, edaphic features, and other factors. Four study sites (LC, PR, FM, and AV) were grassland mixed with forbs in the Antelope Valley of the upper Mojave Desert at or near AVCPR, and two sites (SR) were shrub-grassland ecotones in the foothills of Santa Barbara Co. Of these, only site PR (from AVCPR) supported annuals. The remaining annual populations were from sage scrub habitat in Riverside (NH, EM), and coastal San Diego Counties (CB). Mean temperatures of winter months vary among sites (Table 2), and were used to guide choice of chilling and incubation temperatures. The domesticated population (Dom) has been repeatedly planted and harvested for commercial seed production in Oregon for at least 20 years. The original source population for Dom is unknown, but thought to have been from southern California. The garden population RV01 was plant-

TABLE 2. MEAN DAILY MINIMUM, MAXIMUM, AND MEDIAN TEMPERATURES FOR SOUTHERN CALIFORNIA WEATHER STATIONS NEAR STUDY POPULATIONS.

Closest weather station location	Study population	Mean min/max temperature °C (median temperature)	
		December	January
Lake Cachuma (1952–2000)	SR	3.6/19.3 (11.5)	3.7/18.5 (11.1)
Lancaster (1945–1960)	AV, FM, LC, PR	−1.8/14.9 (6.5)	−1.9/13.8 (5.9)
San Diego (1940–1960)	CB	9.5/19.6 (14.5)	8.1/18.3 (13.2)
San Jacinto (1948–2000)	NH	1.1/19.4 (10.3)	1.1/18.4 (9.7)
Sun City (1973–2000)	EM	1.4/19.8 (10.6)	2.4/18.9 (10.7)

ed before 1990 from an unknown commercial seed source.

*Seed germination experiments.* Six experiments were conducted, with each building on the information gained from previous experiments. General procedures are described below. Details of populations and experiments are in Table 3, including seed age at time of incubation.

*General protocol.* After we collected or received seeds, we stored them in the lab at  $\sim 22 \pm 3^\circ\text{C}$ . Before we obtained seeds from other sources, they had been stored under variable conditions: S&S Seeds stored seeds at ambient conditions in warehouse in coastal, Santa Barbara Co.; Fox and Crossman stored seeds in offices; domesticated seeds were stored under unknown conditions before purchase in June 2000. All wild site collections, including those from S&S Seeds, were documented.

For all experiments, we chose visibly undamaged, plump seeds of uniform shape, and which had obtained a brown to blackish brown color. Seeds were always randomly assigned to treatments (described below). For incubation, one filter paper (Whatman No. 1, 90 mm) was used per petri-dish (Fisher, polystyrene,  $90 \times 15$  mm). Immediately before incubation, for treatments Con, S, H, SH, and Q (below), we placed seeds on filter paper moistened with 2 ml of pH7.5 filter sterilized tap water (hereafter “water”). For treatments L, W, and N, we placed seeds on filter paper moistened with 2 ml of the treatment solution. Unless otherwise indicated, incubation then occurred under a diurnal cycle of 12 hr/22°C and 12 hr/12°C (henceforth 22/12°C). We incubated seeds in winter (excepting Exp. 1 & 2) when they would be germinating in nature to control for any seasonal cycling of dormancy under shelf conditions (see Baskin and Baskin 1998). We aged seeds at least 8 mo in the lab except when testing for after-ripening (Exp. 6), considered here as a period of embryo maturation following seed harvest that occurs before seeds can germinate (Nikolaeva 1969).

For cold treatment, seeds were placed in dishes between two filter papers and either left dry or moistened (see below). Before cold treatment or incubation, dishes were individually wrapped in alu-

minum foil to exclude light and placed in sealed plastic bags to prevent moisture loss or gas exchange between treatments. Cold treatments and incubation took place in the dark because light was reported to inhibit germination of California poppy (Goldthwaite et al. 1971).

We confirmed that light inhibits germination in wild-collected seeds but not in domesticated seeds. We tested the effect of light on germination by incubating 100 moistened seeds from each of four wild and one domesticated population in light (no foil wrap) vs. dark (foil wrapped) under alternating 11 hr days and 13 hr nights (temperature ranged 10–20°C). After 19 days, mean germination under light was 11.7%, 3.6%, 3.2%, 5.7%, and 99%, while germination in the dark was 29.3%, 16.5%, 25.8%, 100%, and 100% for populations EM00, PR01, Pala01, RM01, and Dom, respectively (RM01 = perennial from coastal San Luis Obispo County; Pala01 = annual from inland San Diego County).

At harvest, we scored radicle emergence of at least 1 mm as successful germination. Any remaining, ungerminated seeds were counted and assayed for viability with 2,3,5-triphenyl tetrazolium chloride (TTC) (Fischer), a metabolic indicator dye. Seeds were pierced with a probe, stained by soaking overnight in a 1.0% TTC solution (Kitchen and Meyer 1992), then dissected under a dissecting microscope. A seed was scored as viable if more than two thirds of its embryo stained dark pink or red. Live, ungerminated seeds were considered dormant. The proportion of viable seeds in each dish was ((#germinated seeds + #viable ungerminated seeds)/total # seeds) and proportion germinated was (#germinated seeds/#viable seeds), thereby standardizing germination to the response of viable seeds.

*Fire treatments.* Dry fire treatments (S, H, SH) were given before any temperature treatments whereas wet fire treatments (N, L, W, Q) were given after temperature treatments in the first two experiments. Thereafter, wet fire treatments were given before temperature treatments.

**S (dry smoke):** Smoke stimulates germination in many species and can be applied by various methods. Here, we applied cool dry smoke directly to



TABLE 3. TREATMENTS AND SEED COLLECTIONS USED FOR EXPERIMENTS 1-6. All experiments included controls where seeds were not exposed to cold and kept dry until incubation. See Table 1 for population codes. Seed age is time from seed collection to incubation and is rounded to nearest month—"fresh seed"  $\leq 8$  months old; "young seed" = 9-10 months old; and "aged seed"  $> 2$  years old. \* Exp. 1 and 2 ran concurrently and shared overlapping data for seed populations Dom, LC98, CB97, and NH98. \*\* No cold-shock—seeds not subjected to cold-shock were placed in incubator after soaking. \*\*\* Many seeds germinated under cold treatment of  $> 4^{\circ}\text{C}$ . \*\*\*\* Incubated for 11 hr/13 hr at given temperatures (Exp. 1-5 were incubated at 12 hr/12 hr).

	Exp. 1	Exp. 2*	Exp. 3	Exp. 4	Exp. 5	Exp. 6
Seed Populations (seed age at incubation):	Dom ( $> 1$ yr, $< 3$ yr) LC98 (2 yr 3 mo) CB97 (3 yr 3 mo) NH98 (2 yr 3 mo)	DOM ( $> 1$ yr, $< 3$ yr) LC98 (2 yr 3 mo) PR95 (5 yr 3 mo) CB97 (3 yr 3 mo) NH98 (2 yr 3 mo) FM96 (4 yr 3 mo)	AV00 (8 mo) PR96 (4 yr 8 mo) CB97 (3 yr 8 mo) NH98 (2 yr 8 mo) FM96 (4 yr 8 mo) EM98 (2 yr 8 mo)	AV00 (10 mo) PR00 (10 mo) NH00 (10 mo) EM00 (10 mo)	NH98 (2 yr 9 mo) EM00 (9 mo)	NH01 (2, 4, and 8 mo) FM01 (2, 4, and 8 mo) PR01 (2, 4, and 8 mo) SR101, SR601 (2, 4, and 8 mo) RV01 (2 mo)
Fire treatments:	Con, L, W, N, Q (1:50, 20 hr)	Con, L, W, N, Q (1:50, 20 hr), S, H, SH	Con, S, mQ (1:50, 12 hr)	Con, S, mQ (1:50, 12 hr)	Con-dry, Con-wet, mQ (three dilu- tions: 1:50, 1:25, 1:10; 12 hr)	Con, mQ (1:50, 12 hr) for all ages
Cold treatment:	wet-cold moist-cold dry-cold no-cold	moist-cold no-cold	moist-cold dry-cold no-cold	moist-cold dry-cold no-cold	Cold-shock No cold-shock**	subset of 4 and 8 mo seeds given moist- cold 4 mo @ $3.5^{\circ}\text{C}/(4$ wk) 8 mo @ $3^{\circ}\text{C}/(2$ wk)
Temperature/(Duration) Fire and cold treatment or- der:	$2-4^{\circ}\text{C}/(4$ wk) wet fire treatments after cold	$2-4^{\circ}\text{C}/(4$ wk) wet fire (L, W, N, Q) after cold dry fire (S, H, SH) before cold	$4-9^{\circ}\text{C}$ (7)/(8 wk) dry and wet fire be- fore cold	$4.5^{\circ}\text{C}/(6$ wk) dry and wet fire be- fore cold	$2^{\circ}\text{C}/(48$ hr) mQ and Con-wet be- fore cold-shock	mQ before cold
Seeds per plate/no. of plates:	30/3	30/3	30/5	20/5	25/5	20/5
Incubation temperature:	$22/12^{\circ}\text{C}$	$22/12^{\circ}\text{C}$	$22/12^{\circ}\text{C}$ ***( $4-9^{\circ}\text{C}$ )	$18/6^{\circ}\text{C}$ ***( $4.5^{\circ}\text{C}$ )	$22/12, 18/6,$ constant $7.5^{\circ}\text{C}$	**** $18/6^{\circ}\text{C}$
Incubation duration:	20 d	20 d	20 d	14 d	19 d	15 d

dry seeds as per Keeley and Fotheringham (1998b). We placed dry seeds in small plastic dishes in a large glass chamber. A 500 ml airtight metal can was filled 2/3 full with equal portions of air-dried *Avena fatua* L., *Bromus madritensis* L., *B. diandrus* Roth, *Lessingia flaginifolia* (Hook. & Arn.) M. A. Lane, and *Nassella pulchra* (A. Hitchc.) Barkworth. The vegetation was ignited, and the smoke was transferred into the glass chamber with forced air through a long tube. The chamber was filled with the cooled smoke for 30 seconds, then sealed, and seeds were smoked for five minutes. Our preliminary experiments with domesticated poppy seeds showed that smoking up to 15 minutes does not affect seed viability.

**H (heat):** A brief heat shock has been shown to enhance germination of numerous species (Keeley 1991; Baskin and Baskin 1998), while killing or inhibiting germination of heat-sensitive seeds. To explore *E. californica*'s response to temperatures similar to those that may be experienced by buried seeds during a fire, we heated dry seeds in open Pyrex beakers in a forced air oven at 85°C for 10 minutes. Preliminary trials using a temperature assay range of 70–115°C demonstrated that viability of both wild and domesticated seeds decreased at 115°C, but not all seed populations lost viability at 85°C/10 min (Feist and Montalvo, unpublished data).

**SH (smoke + heat):** A random subset of dry-smoked seeds was heated as in **H**.

**N (nitrogen):** Levels of available N as nitrate have been shown to increase after fire (Sweeney 1956; Franco-Vizcaíno and Sosa-Ramirez 1997), a chemical shift which enhances germination in some species (Thanos and Rundel 1995; Baskin and Baskin 1998). Also, *E. californica* tends to respond positively to disturbance, which in turn is positively correlated with nitrogen availability. We used a solution of 10 mM KNO<sub>3</sub> (Fischer) which has been used successfully to stimulate germination in some fire-following species (Thanos and Rundel 1995; Keeley and Fotheringham, 1998b) to moisten seeds.

**L (leached charrate):** A leachate of the charred remains of plant material enhances germination in some species (Keeley 1991), and simulates water transporting charred plant particles to the seed. We prepared charrate for adding to seeds by burning equal portions of air-dried vegetation (same as in S) until blackened but not ashed. This material was ground and added to water (5 g per 100 ml), stirred overnight, then filtered through several layers of cheesecloth (modified from Keeley 1991).

**W (smoke water):** In this smoke treatment, water picks up smoke particles/chemicals and transfers them to the seed (Keeley and Fotheringham 1998b). We filled an airtight 500 ml can with one of the vegetation types (see S above), set the material on fire, and forced the smoke to bubble through 1 liter of water via a tube. Dried material of each species

(S above) was burned in series until all the material was completely blackened (1–5 minutes).

**Q (liquid smoke):** Commercially produced “liquid smoke” products enhance germination in many plant species, and one such product has been used successfully in Australia to increase germination on mine reclamation sites (Roche et al. 1997b). We obtained commercial liquid smoke (Regen 2000 Smokemaster® Seed Germination Solution, Regen, Glasgow, KY) made from passing smoke through water and concentrating it.

In Exp. 1–2, we soaked seeds after their cold treatments (or after dry control) in a dilution of 1:50 (Regen 2000:water) for 20 hours. This treatment was modified for subsequent experiments. In the first modification (mQ-1), seeds were soaked in a dilution of 1:50 for 12 hours, then air dried at room temperature. Seeds were then subjected to appropriate cold treatments *after* smoke treatment (Exp. 3–4). The second modification (mQ-2) explored the effects of liquid smoke concentration (Exp. 5, below). Although the manufacturer recommends using a 1:10 dilution, a 1:50 dilution had been used in order to decrease the risk of harming seeds with high liquid smoke concentrations. To assess the effects of dilution strength on germination, we soaked seeds 12 hr in either a 1:50, 1:25, or 1:10 dilution, then transferred wet seeds to the appropriate cold-shock treatment (see below).

**Con (control for fire treatments):** No fire treatments were given, and seeds were subjected to the appropriate temperature and moisture treatments (below).

#### *Temperature and moisture treatments.*

**Cold:** Seeds in petri dishes between two filter papers were subjected to prolonged cold temperatures in a cold chamber (ranging from two to eight weeks) while either moist or dry. Seeds were moistened with 2 ml of fluid (moist-cold), 3 ml of fluid (wet-cold), or left dry (dry-cold). Wet-cold treatment provided free water for rapid imbibing, moist-cold provided for slower imbibing and high relative humidity, while the dry method tested whether poppy seeds can be affected by cold treatment when dry. In addition, Exp. 5 tested the effects of a brief cold-shock (48 hours at 2°C) instead of prolonged cold treatment.

Cold treatment was intended to occur near or below 4°C. Problems with one cold room resulted in higher cold-treatment temperatures during Exp. 3 (see below), averaging near 7°C (range 4–9°C), which resulted in a positive germination response and provided the impetus to test variation in incubation temperature in Exp. 5.

**No-cold (control for cold and moisture treatments):** For dry, no-cold conditions, henceforth “no-cold”, we stored seeds dry at room temperature until moistened and incubated.

*Experiments.* All experiments included a control treatment, for which seeds received no fire or cold

treatments prior to incubation. At the time of incubation, those seeds collected in spring 2001 were between 2–7.5 months old (henceforth “fresh seeds”), seeds collected in 2000 were between 8–10 months old (henceforth “young seed”), and all other wild seeds were > two years old (henceforth “aged seed”).

Experiment 1 and Exp. 2 were run concurrently and were overlapping subsets of one experiment. In Exp. 1, we examined germination response of three “aged seed” populations and domesticated seeds to cold treatment at three different moisture levels (wet, moist, and dry) in combination with five “wet” fire-effects treatments (Table 3). The wet fire treatments were applied after seeds had been cold-treated.

In addition, for Exp. 2 we added three “dry” fire treatments (S, H, and SH) under three cold treatments (moist-cold, dry-cold, no-cold treatment) and on seeds of two additional wild populations (PR95 and FM96, for a total of six populations). The application of dry fire treatments before seeds were chilled, simulated the natural sequence of events in the wild. The chilling temperature ranged from 2–4°C; most often close to 2°. For both Exp. 1 and Exp. 2, incubating seeds were checked using dim green lights after 3, 8, 13, and 20 d of incubation. No increase in germination was seen after 13 days.

In Exp. 3, we investigated five aged and one young seed population, increased the number of replicates from three to five petri-dishes to increase statistical power, and examined the response of wet and dry smoke (mQ-1 and S) to a longer 8 wk cold treatment and a more natural sequence of smoke and cold events (Table 3). Both the S and mQ treatments were applied before seeds were subjected to moist cold treatments. The cold room cycled between 4–9°C, and was mostly just below 7°C. After cold treatment, any germination was tallied, and ungerminated seeds were transferred into new dishes with fresh filter paper, moistened with 2 ml water, and incubated for 20 days before scoring germination and viability.

Experiment 4 assessed germination of young seeds collected in the same year to investigate their response to smoke and cold treatments (Table 3). Data from Exp. 3 suggested that young seeds (<1 yr) may be less dormant or have dormancy more easily broken than aged seeds (2+ yr) which could complicate experiments with mixed age seeds. Extended shelf storage can trigger secondary dormancy in some species while decreasing dormancy in others (Roche et al. 1997a; Baskin and Baskin 1998).

In Exp. 5 we tested different concentrations of liquid smoke (mQ-2), different incubation temperatures, and the effect of a brief cold-shock on germination and viability of two populations, one with young seeds and one with aged seeds (Table 3). Different incubation temperatures (22/12, 18/6, and 7.5°C constant) were tested to determine if lower

incubation temperatures improved germination, given that germination was possible and sometimes higher at quite low temperatures (Exp. 3). In addition, we subjected half the seeds to a 48 hr cold-shock at 2°C instead of prolonged cold because short cold treatments are sometimes sufficient for either breaking or inducing dormancy and are ecologically realistic within *E. californica*'s range. Finally, to discern between the possible effects of soaking which may leach germination inhibitory chemicals from seeds, and the effects of wet fire treatments, we added a wet-control treatment (12 hr soak in water).

We used annual population EM00 for the full Exp. 5. In addition, seeds from the deeply dormant NH98 population were run with only a wet-control and with 18/6°C as the incubation temperature (based on incubation temperature with highest germination in Exp. 4) to see if germination could be improved with higher or lower concentration of liquid smoke.

We ran Exp. 6 to test if recently collected “fresh” wild and domesticated California poppy seeds germinate at different rates with and without smoke treatment over the course of several months after fruit dehiscence. If seeds require lengthy after-ripening or if in the lab they experience an annual cycle of dormancy followed by conditional dormancy or loss of dormancy as expected under natural conditions, then these behaviors could affect the outcome of germination experiments run at different seed ages or times of the year. We collected seeds into paper envelopes in May 2001 from four wild populations (perennial FM and SR; annual NH and PR, Table 3), and from garden plants in Riverside (RV—started from commercial seed source > 10 years earlier, Table 3). Six weeks after collection and shelf storage, we randomly sorted seeds into microcentrifuge tubes, and then tested at 2, 4, and 7.5 months (herein “8” mo) following seed harvest. We incubated controls and liquid smoke-treated seeds (mQ-1) in the dark at alternating 18°C/6°C for 11/13 hours for 15 days and scored germination and viability. Subsamples of smoked seeds aged 4 mo and 8 mo were given moist-cold treatments (4 wk at 3.5°C and 2 wk at 3°C, respectively) before incubation.

**Data analysis.** Data were analyzed with ANOVA using Proc GLM of SAS (Release 6.12). In all models, source POPULATION was a random effect while COLD (e.g., cold vs no-cold), FIRE (e.g., smoke, heat, nitrate, water, etc.), or AGE treatments were fixed effects. Response variables included proportion of viable seeds germinated/dish, and the proportion of viable seeds out of total seeds/dish. Dishes were the replicates. Before analysis, all data were angularly transformed ( $\arcsin(\text{proportion})^{1/2}$ ) to enhance the normality of the residuals. We used either Duncan's Multiple Range test or Tukey's test for *posteriori* comparisons among means. In mod-

els where we found significant interactions among main effects, we ran separate analyses on each population or treatment depending on structure of the interaction and the particular question. Given the mixed model ANOVAs, we used the RANDOM statement in SAS to calculate the denominator mean squares for F-tests using the Satterwaite model.

## RESULTS

*General patterns.* Over experiments, seed dormancy (Table 4) and the effect of potential dormancy breaking treatments varied substantially among years of collection and among populations (Tables 5, 6; Fig. 1–5). The domesticated commercial (Dom) and garden (RV) populations were the only ones with no seed dormancy (Table 4). Other populations ranged from 41% to 100% dormant under control conditions. In general, young seeds collected in 2000 had higher germination in controls and higher germination following treatment with liquid smoke than aged seeds (mean 65% vs. 92%; Table 6).

There were differences in seed dormancy among young (year 2000) collections from the Antelope Valley, with much lower dormancy of the perennial AV00 and FM00 than the annual PR00. Aged seeds had uniformly high dormancy (range 93–100%).

Seed viability also varied among wild collections and ranged from 54–100% following treatments (Table 4). Populations NH98 and FM96 showed different levels of viability between experiments, possibly because of differences among technicians in sorting bulk seeds to be used in experiments. The range in viability shows the importance of basing % germination on live seeds rather than total seeds.

There were highly significant effects of fire and cold treatments and significant population effects. In addition, the many significant two and three way interactions between FIRE, COLD, AGE, and POPULATION main effects (Table 5) indicate variation among populations in response to at least some treatments. Because of this complexity, we present results of each experiment separately and break up analyses to examine interactions and effects of fire, cold, and age treatments.

Given their lack of seed dormancy, we did not statistically compare Dom and RV with wild populations. The domesticated seeds had nearly 100% germination and viability in all treatments except those involving heat. In addition, unlike the dormant-seeded populations, Dom seeds germinated during cold treatment at 2–4°C. Separate analysis of population Dom seeds under the no-cold regime showed that there was no significant difference among the Con, S, N, W, L, or Q treatments. However the H and SH treatments reduced germination significantly suggesting that heat treatment inhibited germination and even killed some seeds. Viability of seeds from the H and SH treatments ranged from 64–100%, compared to 100% in controls.

*Experiment 1—Effect of wet-fire and cold treatments (moist-cold, wet-cold, dry-cold, and no-cold).* Analysis of germination from the three study populations of different regions (annual NH98, perennial LC98, and annual CB97) revealed significant main effects and interactions except POPULATION and FIRE  $\times$  POPULATION (Table 5). When germination was analyzed for each population separately, FIRE, COLD and FIRE  $\times$  COLD were still significant for each population (all P values  $\leq$  0.0113). This significant interaction shows that each population responded to the set of treatments differently, obscuring whether any particular cold treatment or fire treatment resulted in the highest germination. However, for all populations, the no-cold regime resulted in the highest mean germination (Fig. 1), suggesting that the 2°C cold treatment was cold enough to slightly inhibit germination in the three populations examined.

We also analyzed germination response separately by level of cold treatment and found no significant FIRE  $\times$  POPULATION interactions, and in the wet-cold analysis we found no significant FIRE or POPULATION effects (Fig. 1). In the moist-cold treatment, annual NH98 had significantly higher germination than perennial LC98 and annual CB97 seed populations, while in the no-cold regime CB97 seeds had significantly higher germination than LC98 and NH98 (Fig. 1). Inland NH98 seeds appear to germinate under cold conditions more readily than coastal CB97 seeds. There were significant effects of FIRE treatment only in the dry-cold and no-cold regimes, potentially because liquid fire treatments were applied after chilling in moist-cold and wet-cold. In no-cold and dry-cold, treatment Q resulted in the highest germination, although Q and W were not statistically different under the no-cold control conditions (Fig. 1).

With ANOVA of Experiment 1, we examined the effect of treatments on seed viability to reveal if some treatments harmed seeds. We found no significant main effects, but the COLD  $\times$  FIRE  $\times$  POPULATION interaction was significant ( $F_{24, 120} = 1.67$ ;  $P < 0.04$ ), suggesting that seed viability of different populations was affected differently by the cold and fire treatments. After running viability data separately by population, no significant effects of COLD or FIRE treatments were found for CB97. Population LC98 showed a significant effect of FIRE treatment ( $F_{4, 39} = 3.07$ ;  $P = 0.027$ ) and a FIRE  $\times$  COLD interaction ( $F_{12, 40} = 2.26$ ;  $P = 0.028$ ). COLD had a significant effect on NH98 ( $F_{3, 40} = 6.76$ ;  $P < 0.001$ ), with the no-cold regime more viable than all other cold treatments. No other effects were significant. Overall, the wet-cold treatment resulted in the lowest germination in NH98 (Fig. 1).

When viability was analyzed for each cold regime separately, the only significant effect of POPULATION was in the no-cold treatment ( $F_{2, 8} = 4.73$ ;  $P = 0.044$ ), with NH98 having greater via-

TABLE 4. DORMANCY AND VIABILITY OF CONTROLS (FIRE TREATMENT "CON" AND "NO-COLD") FOR ALL SEED POPULATIONS. Means ( $\pm 1$  SD) are backtransformed and population abbreviations are as in Table 1. The larger the means, the more dormant and more viable the seeds, respectively. Abbreviations: Pop = population; A = annual; P = perennial; — = not applicable. (n = five replicate dishes except for Exp 1–2 where n = 3). Data for 8 mo-old seeds are reported for Exp. 6 except for RV01 where 2 mo-old seeds were used. Seed age is in Table 3.

Pop code	Life- history	% Seed dormancy					% Seed viability				
		Exp 1–2	Exp 3	Exp 4	Exp 5	Exp 6	Exp 1–2	Exp 3	Exp 4	Exp 5	Exp 6
CB97	A	85 (12.9)	99 (4.3)	—	—	—	63 (12.0)	72 (6.9)	—	—	—
EM98	A	—	91 (3.7)	—	—	—	—	75 (5.9)	—	—	—
EM00	A	—	—	—	68 (12.6)	—	—	—	—	80 (0.1)	—
PR95	A	94 (12.7)	—	—	—	—	86 (8.4)	—	—	—	—
PR96	A	—	100 (0)	—	—	—	—	87 (4.3)	—	—	—
PR00	A	—	—	86 (0.9)	—	—	—	—	91 (0.5)	—	—
PR01	A	—	—	—	—	57 (11.8)	—	—	—	—	98 (2.7)
NH98	A	88 (15.4)	88 (7.5)	—	92 (13.6)	—	85 (2.3)	54 (6.7)	—	75 (0.01)	—
NH00	A	—	—	70 (5.3)	—	—	—	—	84 (1.6)	—	—
NH01	A	—	—	—	—	92 (8.4)	—	—	—	—	94 (6.5)
LC98	P	93 (23.3)	—	—	—	—	78 (7.7)	—	—	—	—
AV00	P	—	48 (11.6)	41 (0.7)	—	—	—	95 (4.3)	95 (2.2)	—	—
FM96	P	96 (1.7)	94 (4.5)	—	—	—	89 (3.9)	74 (8.6)	—	—	—
FM00	P	—	—	46 (0.8)	—	—	—	—	98 (1.5)	—	—
FM01	P	—	—	—	—	59 (11.1)	—	—	—	—	96 (7.3)
SR01	P	—	—	—	—	58 (10.6)	—	—	—	—	93 (5.7)
RV01	P	—	—	—	—	1 (2.1)	—	—	—	—	97 (2.7)
Dom	P	0 (0)	—	—	—	—	100 (0)	—	—	—	—

TABLE 5. ANOVA TABLES FOR GERMINATION RESPONSE IN EXPERIMENTS 1–6. For Experiments 1–4 and 6, full models are shown; COLD refers to cold treatments, and FIRE refers to fire treatments (see Table 3). For exp. 5, only results for population EM00 are presented; SHOCK, INCUBATION, and FIRE refer to those treatments as noted in Table 3 under Cold, Incubation, and Fire treatments, respectively. Num and Den df are numerator and denominator degrees of freedom, respectively. Exp. 5 is a fixed effects model so Den df is that of error term.

Source	Num df	Den df	F	P <
EXPERIMENT 1				
Cold	3	6	49.89	0.001
Fire	4	8	17.41	0.001
Population	2	5.3	1.40	0.325
Cold × Fire	12	24	6.76	0.001
Cold × Population	6	24	4.94	0.002
Fire × Population	8	24	0.77	0.635
Cold × Fire × Population	24	120	1.67	0.038
Error	120			
EXPERIMENT 2				
Cold	1	4	12.47	0.024
Fire	7	28	16.46	0.001
Population	4	4.6	1.67	0.302
Cold × Fire	7	28	9.32	0.001
Cold × Population	4	28	5.48	0.002
Fire × Population	28	28	1.41	0.184
Cold × Fire × Population	28	160	2.38	0.001
Error	160			
EXPERIMENT 3				
Cold	2	10	9.17	0.001
Fire	2	10	203.07	0.001
Population	5	7.2	233.20	0.001
Cold × Fire	4	20	2.00	0.096
Cold × Population	10	20	1.34	0.276
Fire × Population	10	20	1.41	0.244
Cold × Fire × Population	20	216	2.27	0.002
Error	216			
EXPERIMENT 4				
Cold	2	6	9.35	0.001
Fire	2	6	231.81	0.001
Population	3	6.8	5.26	0.034
Cold × Fire	4	12	6.18	0.001
Cold × Population	6	12	2.55	0.079
Fire × Population	6	12	20.09	0.001
Cold × Fire × Population	12	144	0.59	0.847
Error	144			
EXPERIMENT 5				
Shock	1		4.32	0.040
Incubation	2		7.01	0.001
Fire	4		220.20	0.001
Shock × Incubation	2		1.12	0.328
Shock × Fire	4		0.45	0.775
Incubation × Fire	8		0.24	0.983
Shock × Fire × Incubation	8		0.96	0.468
Error	120			
EXPERIMENT 6				
Age group	2	8.02	8.05	0.012
Fire (Con vs. mQ)	1	4	23.08	0.009
Population	4	7.74	2.35	0.144
Age × Fire	2	8.08	9.04	0.009
Age × Population	8	8	4.57	0.023
Fire × Population	4	8.05	6.17	0.014
Age × Fire × Population	8	116	1.78	0.088
Error	116			

TABLE 6. SUMMARY OF MEAN % GERMINATION OF YOUNG VS. AGED SEEDS COMPARING RESPONSE TO DRY SMOKE (S), LIQUID SMOKE (MQ), AND WATER CONTROLS ACROSS EXPERIMENTS. Population abbreviations as in Table 1. No-cold = germination under no-cold (and no cold-shock) treatments. Moist-cold = moist-cold treatments as in Table 3. Values in **bold** represent higher germination under moist-cold compared to no-cold for the same smoke treatment. \* = liquid smoke concentrations of 1:10 (all others were 1:50); \*\* = Exp. 2 had liquid smoke applied after cold treatment. Dashes represent absence of treatment. See Table 3 for seed age.

Pop code	Exp	Mean % germination					
		Moist-cold			No-cold		
		Control	Liquid smoke	Dry smoke	Control	Liquid smoke	Dry smoke
LC98	2	1.5	—**	<b>55.4</b>	7.3	37.8	29.4
AV00	3	<b>54.5</b>	<b>86.8</b>	<b>70.6</b>	52.6	83.3	60.2
AV00	4	45.8	<b>88.2</b>	<b>68.7</b>	58.9	82.9	49.7
PR95	2	0	—**	42.3	6.3	46.5	44.0
PR96	3	0	2.9	0	0	3.6	0
PR00	4	<b>14.0</b>	<b>70.8</b>	<b>48.7</b>	13.7	65.5	21.5
NH98	2	<b>24.4</b>	—**	<b>24.1</b>	11.9	41.9	19.3
NH98	3	<b>23.8</b>	<b>47.5</b>	<b>25.6</b>	11.8	33.8	2.5
NH98	5	—	—	—	7.8 <sup>(wet)</sup>	34.0*	—
NH00	4	<b>33.3</b>	<b>97.2</b>	<b>73.2</b>	29.9	94.9	51.5
FM96	2	0	—**	<b>24.8</b>	3.8	10.5	10.7
FM96	3	3.2	<b>31.9</b>	3.6	4.8	25.6	6.6
FM00	4	44.5	<b>77.8</b>	<b>73.5</b>	53.9	69.7	59.4
EM98	3	<b>28.2</b>	59.4	<b>36.6</b>	9.3	65.2	15.2
EM00	5	—	—	—	31.7	94.6	—

bility than LC98 and CB97 (Tukey's test,  $\alpha = 0.01$ ). Thus, the significant COLD  $\times$  FIRE  $\times$  POPULATION effect of the full model analysis is due in part to population NH98 having much improved viability in the no-cold treatment. This small negative effect of 2°C on viability for NH98, suggests that any ungerminable seeds in the process of viability degradation may have died more readily than such marginal seeds of other populations, thus influencing the germination rate for NH. Otherwise, there was little effect of cold or other treatments on viability.

*Experiment 2: Effect of all fire and cold treatments (moist-cold vs. no-cold).* ANOVA of Experiment 2 germination data showed that all effects were significant except POPULATION and FIRE  $\times$  POPULATION (Table 5). We then broke the analysis down by the two cold treatments because of the significant 3-way interaction of main effects.

In both the moist-cold and no-cold regimes, FIRE, POPULATION and FIRE  $\times$  POPULATION were all significant ( $P < 0.001$ ), so the analysis was further broken down by population for each cold regime separately. Under moist-cold, for all populations except NH98, we found a significant effect of FIRE treatment on germination (all  $F_{7,16} > 4.13$ ;  $P < 0.009$ ), with S producing significantly higher germination. For NH98, mean germination was highest for S, but non-significant (Fig. 2). A Kendall's analysis of the rankings of fire treatment within each population showed a strong association between fire treatment and germination ( $0.01 < P$

$< 0.001$ ). Treatment S had the highest overall ranking, HS and H had the lowest overall rankings (indicating heat reduces germination), while all other treatment rankings were very similar.

Under the no-cold regime, germination of all populations except FM96 was significantly affected by FIRE treatment (all  $F_{7,16} > 6.2$ ;  $P \leq 0.001$ ). A Kendall's analysis of the rankings of treatments within each population showed a strong association ( $P < 0.001$ ) between fire treatment and germination. For all populations, Q produced the highest mean germination, while S and W tied for second place (Fig. 2). Averaged over the five populations, the no-cold controls germinated only 25% as well as seeds treated with liquid smoke (Q). The H and HS treatments were ranked lowest overall. Again, the heat treatments reduced germination. Germination of H treated seeds for the five populations averaged 38% of control seed germination. Q performed best in the no-cold regime, while S produced the highest germination in the cold regime, again suggesting the effect of Q would improve if applied before chilling. This hypothesis was verified in Exp. 3, below.

ANOVA of Exp. 2 viability data showed that POPULATION, FIRE, and COLD were all significant effects (POP  $F_{4,45} = 5.76$ ;  $P = 0.049$ ; FIRE  $F_{7,28} = 4.53$ ;  $P = 0.002$ ; COLD  $F_{1,4} = 12.4$ ;  $P = 0.024$ ). There were no significant interactions (all  $P > 0.11$ ). In the full model, viability was unaffected by all treatments except H and SH, which significantly decreased viability (Duncan's Multiple

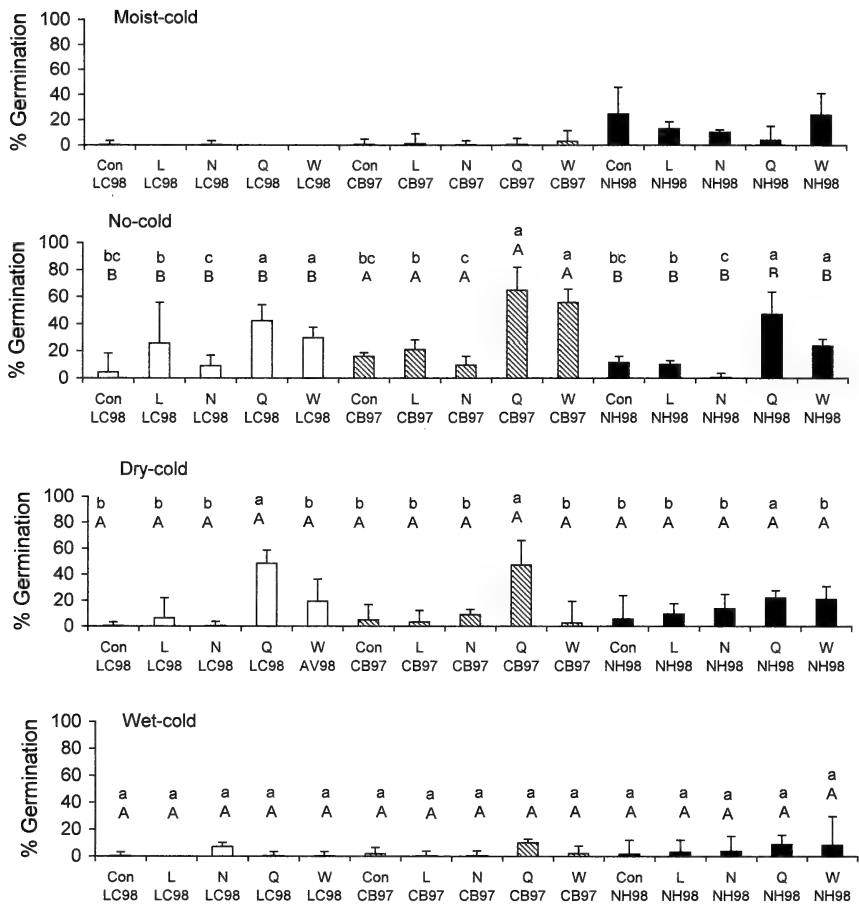


FIG. 1. Experiment 1 backtransformed germination data, analyzed for each population within each cold treatment. Lower and upper case letters represent significant differences between treatments and populations, respectively, based on Tukey's tests ( $\alpha = 0.05$ ). Within each cold treatment, populations or treatments that share a letter are not significantly different. In moist-cold, NH98 had higher germination than CB97 and LC98, but there were no significant effects of fire treatment. Error bars = 1 SD ( $n = 3$ ). Abbreviations: Con = control, L = leached charrate, N = nitrogen ( $\text{KNO}_3$ ), Q = liquid smoke, and W = smoke water.

Range Test, using  $\alpha = 0.05$ ). Viability of SH and H treated seeds for the five populations averaged 6% lower than viability of control seed, compounding the effect of reduced germination. Overall, FM96 had significantly higher viability than all other populations, and CB97 had significantly lower viability than all but population LC98 (Tukey's test,  $\alpha = 0.01$ ) (Table 4).

For remaining experiments, analysis of seed viability will not be presented in detail. Additional treatments had little affect on seed viability.

*Experiment 3: Effect of dry smoke, liquid smoke and moist-cold, dry-cold, and no-cold (smoke before cold).* In Exp. 3, many seeds germinated unexpectedly during moist cold treatment, including some FIRE treatment controls. For populations that germinated during cold treatment, very few of the remaining seeds germinated after shifting to the

warmer incubation period. Therefore, in ANOVA of total % germination, the main effect of COLD represents three treatment levels: moist-cold = incubation at 4–9°C; no-cold = incubation at 22/12°C; and dry-cold = incubation at 22/12°C following 8 wk dry cold treatment.

ANOVA of total % germination showed a significant COLD  $\times$  FIRE  $\times$  POPULATION interaction (Table 5). When data were broken up by population, treatment mQ (modified liquid smoke) produced significantly greater germination than the other treatments in all populations (averaging over fire treatments shown in Fig. 3), but there was a significant COLD  $\times$  FIRE interaction within EM98 and NH98. EM98 and NH98 were the only populations significantly affected by COLD ( $P < 0.0024$ ), and in both cases moist-cold produced higher germination than dry-cold and no-cold (Fig.



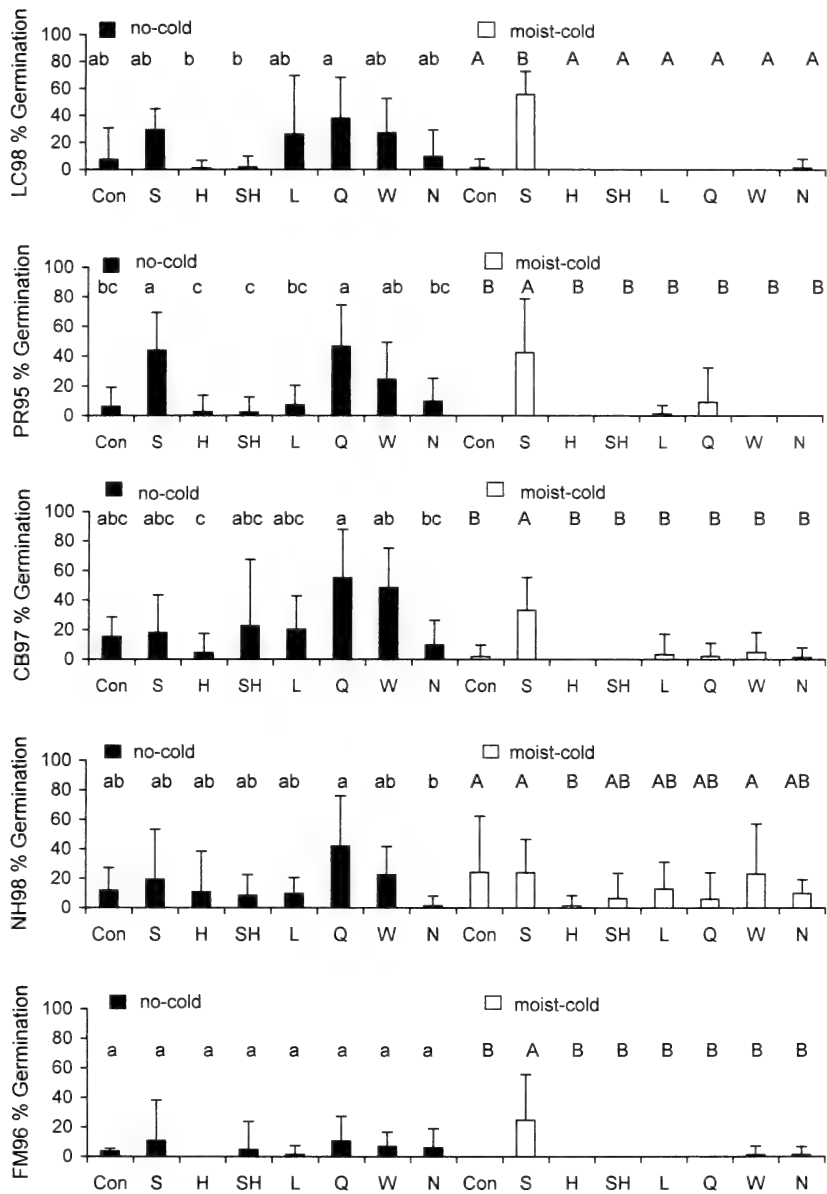


FIG. 2. Experiment 2 backtransformed germination data, analyzed separately for moist-cold and no-cold treatments within each population. Lower and upper case letters indicate significant differences (Tukey's test, alpha = 0.01) occurring between treatments within no-cold and moist-cold regimes, respectively. FIRE treatments that share a letter are not significantly different. Error bars = 1 SD (n = 3). Abbreviations: as in Fig. 1 plus S = dry smoke, H = heat, and SH = smoke plus heat.

3). In a separate analysis by cold regime, there was a significant interaction of FIRE  $\times$  POPULATION in no-cold and dry-cold, likely due to populations CB97 and EM98, for example, having much larger differences between mQ and control treatments than population AV00. However, in all cold treatments, mQ produced the best germination, and was highest for AV00, then EM98, and lowest for PR96.

Evidently, germination decreased as seed age increased.

*Experiment 4: Effect of dry and liquid smoke vs. cold treatments on "young" seeds.* ANOVA of germination data showed that all effects were significant except COLD  $\times$  POPULATION and COLD  $\times$  TREATMENT  $\times$  POPULATION (Table 5). Even

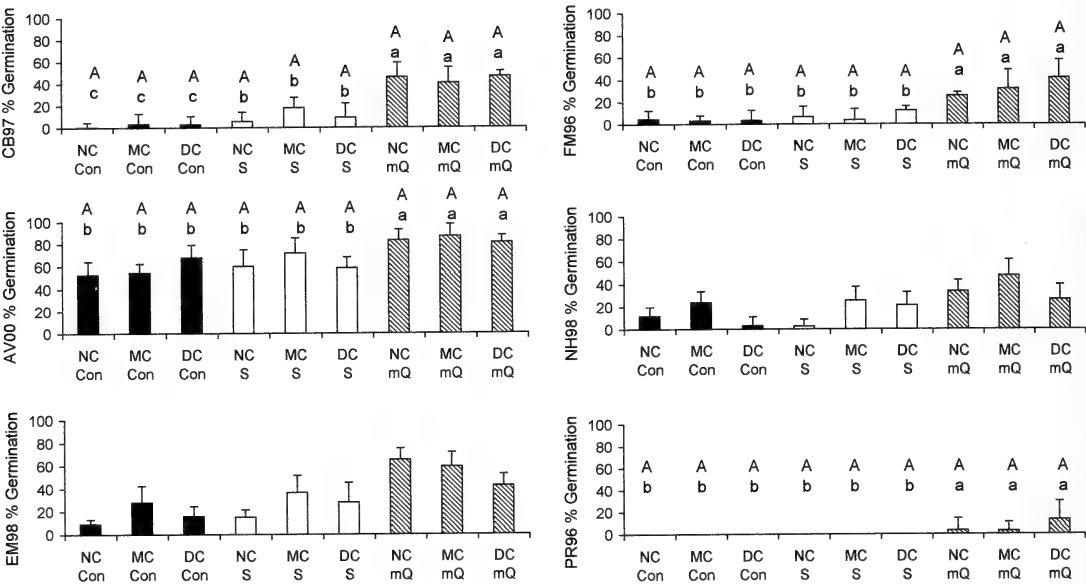


FIG. 3. Experiment 3 backtransformed germination data, analyzed for each population. Upper case and lower case letters indicate significant differences between COLD or FIRE treatments, respectively (Tukey's test, alpha = 0.05). COLD or FIRE treatments that share a letter do not have significantly different germination. For populations EM98 and NH98, no Tukey's tests were run due to significant COLD  $\times$  FIRE interactions. Error bars = 1 SD (n = 5). Treatment abbreviations: Con = control, NC = no-cold, MC = moist cold, DC = dry cold, S = smoke, mQ = modified liquid smoke.

though the strength of different TREATMENTS varied by population and cold treatment, the TREATMENT controls had the lowest mean in 11 of 12 comparisons of population/cold combinations (Fig. 4). The significant interaction of TREATMENT  $\times$  POPULATION appears to be due to the annual populations (NH00 and PR00) having higher seed dormancy and larger differences among treatment means than the perennials (AV00 and FM00).

Because of the significant interactions, we used ANOVA to analyze germination separately for each population. For AV00, there was a significant interaction of COLD  $\times$  TREATMENT ( $F_{4,36} = 3.91$ ;  $P = 0.009$ ), however TREATMENT was highly significant ( $F_{2,36} = 48.70$ ;  $P < 0.001$ ). Germination of AV00 in moist-cold and dry-cold was lowest in fire controls, higher with S, and highest with mQ, but position of no-fire Con and S were switched under no-cold (Fig. 4). For FM00, S and mQ were not significantly different from each other, but both smoke treatments were significantly higher than controls. The trend seen in AV00 was even stronger in the two annual populations (PR00 and NH00; Fig. 4). In all three cold treatments, mQ resulted in significantly higher germination than S, and S resulted in higher germination than Con. Cold treatments were significant only for annuals (PR00  $F_{2,36} = 5.73$ ;  $P = 0.007$ ; and NH00  $F_{2,36} = 4.80$ ;  $P = 0.014$ ) with moist-cold producing significantly higher germination than dry-cold in both cases, and

also higher than no-cold for PR00 (Fig. 4), suggesting a small synergistic effect of cold and smoke.

*Experiment 5: Effect of different liquid smoke concentrations (mQ), incubation temperatures, and cold-shock.* ANOVA was run on the two populations separately because NH98 underwent only a subset of treatments. The full model analysis of EM00 showed significant effects of SHOCK, INCUBATION TEMPERATURE, and TREATMENT, with no significant interactions (Table 5). The 3 mQ concentrations yielded much higher germination than the no-fire controls, and all concentrations performed equally well (Fig. 5). In addition, the two colder incubation temperatures (7.5°C and 18/6°C) resulted in higher germination than warmer incubation (22/12°C; Tukey's test, alpha = 0.05). Seeds readily imbibed fluids and there was no difference between wet and dry controls, indicating leaching of inhibitors is not a factor in success of liquid pre-germination treatments. Finally, cold-shock decreased germination of EM00 relative to no-shock (Fig. 5) but the difference was slight.

ANOVA analysis of the NH98 germination revealed a significant effect of TREATMENT only ( $F_{3,32} = 11.43$ ;  $P = 0.001$ ). Unlike in EM00, germination of NH98 seeds was significantly higher as smoke concentration increased (Fig. 5; Tukey's test, alpha = 0.05), and cold-shock had no effect on germination ( $F_{1,32} = 0.01$ ;  $P = 0.934$ ).

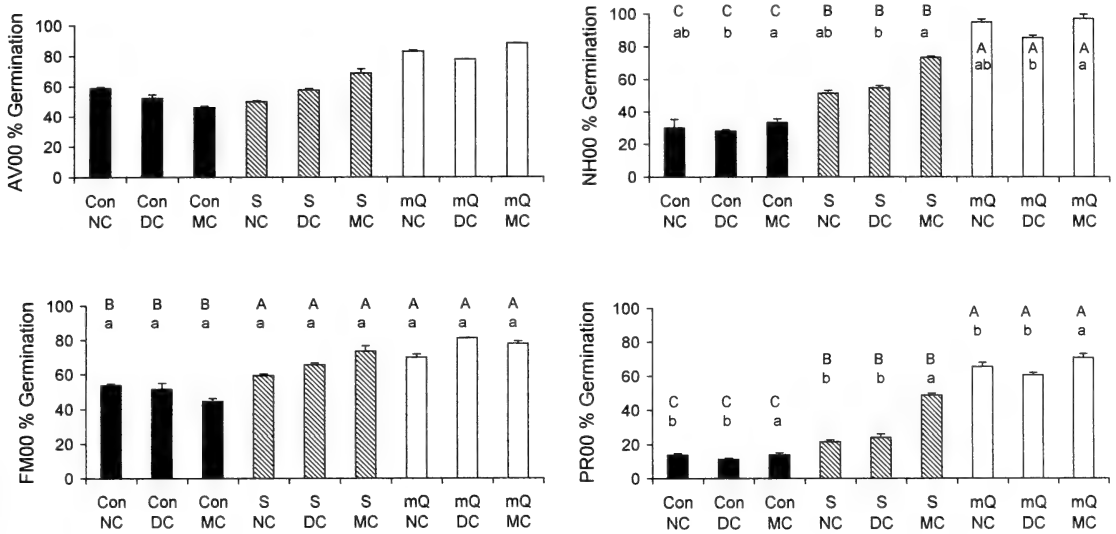


FIG. 4. Experiment 4 backtransformed germination data, analyzed for each population. Upper case and lower case letters indicate significant differences (Tukey's test,  $\alpha = 0.05$ ) among smoke or cold treatments, respectively. Smoke or cold treatments that share a letter do not have significantly different germination. For populations AV00 no Tukey's test was run due to significant COLD  $\times$  smoke TREATMENT interaction. Error bars = 1 SD ( $n = 5$ ). Abbreviations as in Fig. 3.

**Experiment 6: Effect of aging 2–8 months from collection and of liquid smoke (mQ-1) on germination:** The garden RV01 seeds germinated to 99% under both control and liquid smoke conditions at 2 mo of age so we did not continue to examine them at 4 mo and 8 mo, nor was RV included in statistical analysis. We ran ANOVA separately on each wild population because of significant 2-way interactions between population, smoke treatment, and seed age (Table 5). The interactions indicate that populations respond differently to both treatment and aging, either in degree or direction of response. Controls of FM01, NH01, and PR01 had significantly lower germination at all ages than did mQ-1 treated seeds (Fig. 6). Except for FM01, 2-mo old seeds had significantly lower germination than older seeds, but there was usually no difference between germination of 4 mo and 8 mo-old seeds. The strongest evidence for after-ripening was for perennial populations from Santa Barbara County (SR101 and SR601) where there was no increase in germination of mQ-1 treated seeds at age 2 mo, but thereafter mQ-1 treatment resulted in significant increases. This result, together with higher germination of both controls and smoked seeds at 4 and 8 mo age suggests that ~60% of seeds required an after-ripening period of > 2 mo before they were capable of dormancy break and germination (Fig. 6). We also looked at effects of mQ-1 and a cold treatment at 3–3.5°C on 4 and 8 mo-old seeds (Fig. 6). A separate ANOVA of treatment (cold + mQ-1 vs. mQ-1) and age (4 vs. 8 mo) on germination, showed no significant effect of cold treatment or age in PR01 or FM01. However,

cold significantly increased germination in NH01 and SR101 seeds and decreased germination in SR601. Germination was significantly higher for 4 mo-old seeds in these later three populations. Thus cold treatment had an inconsistent effect on germination relative to just smoke-treated seeds both among age groups and among populations.

## DISCUSSION

Our study populations came from a set of contrasting southern California environments. We used seeds of both annual and perennial life-histories and with different levels of seed dormancy. We examined whether cold treatment, some specific components of fire, or some combination enhances germination of dormant seeds, and found important direct effects of smoke. This is important because historically, fire has been naturally occurring and periodic in both shrub and grasslands of California, (Parsons 1981; Keeley 1991) where poppies occur. Additionally, for thousands of years prior to European settlement, indigenous tribes of southern California managed many areas with fire to encourage growth of animal forage as well as certain food and textile plants (Bean and Lawton 1973; Timbrook et al. 1982; Lewis 1993). With such repeated exposure to fire, we expect that many species that have not been considered fire followers may, nonetheless, respond to chemical constituents of fire. Even in desert areas that do not have a history of frequent wildfire, the incidence of fire is increasing due to fuel loading by invasive grasses coupled with increasing human activity (Brooks 1999), underscor-

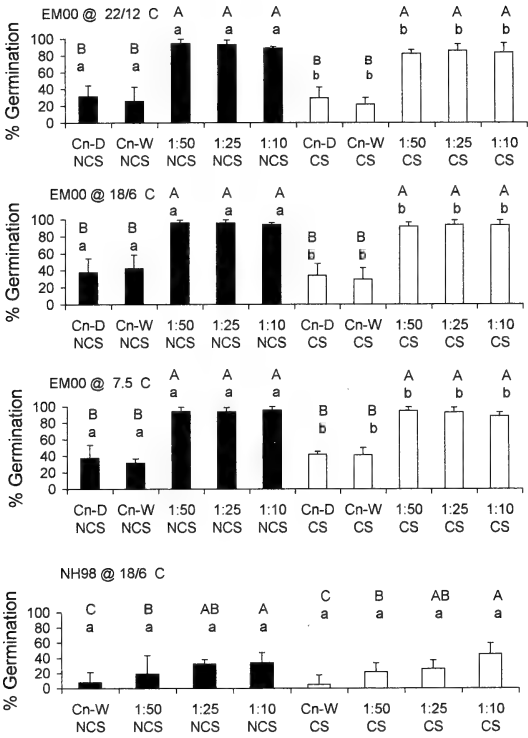


FIG. 5. Experiment 5 backtransformed germination data, analyzed for each population and incubation temperature separately. Upper case letters indicate significant differences (Tukey's test, alpha = 0.05) among the three liquid smoke (mQ) concentrations. Lower case letters designate ANOVA result for differences between cold-shocked (CS) and no-shock control (NCS) seeds. Error bars = 1 SD (n = 5). Solid bars are NCS and open bars are CS treatments. Cn-D = dry control; Cn-W = wet control.

ing the need to understand the effects of fire on plant reproduction.

**Fire treatments.** Smoke applied dry or wet was successful in substantially increasing germination of all dormant seeded populations, sometimes by as much as three to four fold over controls. Dry smoke (S), smoke water (W), and liquid smoke (Q, Qm-1, Qm-2) all improved germination substantially over controls showing that smoke can break dormancy when delivered to seeds in various ways. Because seeds readily imbibed water, the mechanism for the effect of smoke on germination in this species may not involve changing the structure of the seed coat cuticle as has been detected for *Emmenanthe penduliflora* (Egerton-Warburton 1998; Keeley and Fotheringham 1998a). It is possible that ethylene or other components of smoke influence seed germination in California poppy, but this needs further study. Both dry smoke and smoke water contain ethylene (Sutcliffe and Whitehead 1995), which is known to promote germination by several different mechanisms and can sometimes overcome secondary dormancy or particular temperature requirements for germination (Corbineau and Côme 1995; Baskin and Baskin 1989).

Commercially produced liquid smoke gave the best results and outperformed dry smoke except when applied after chilling. In each case, the seeds responded best to the most natural sequence of events. Any "smoke" event would likely occur in the dry season before the winter rains or as a result of rain carrying smoke particles from the soil surface to the seedbank in late fall or early winter. Results were more erratic for dry smoke than for liquid smoke treatments, possibly because adsorption of dry smoke among experiments is more difficult to control.

Other fire treatments were less effective or even inhibited germination. We found no significant benefit of charred plant leachate (L), or nitrate ( $KNO_3$ ) on germination. It is possible that charate and  $NO_3$

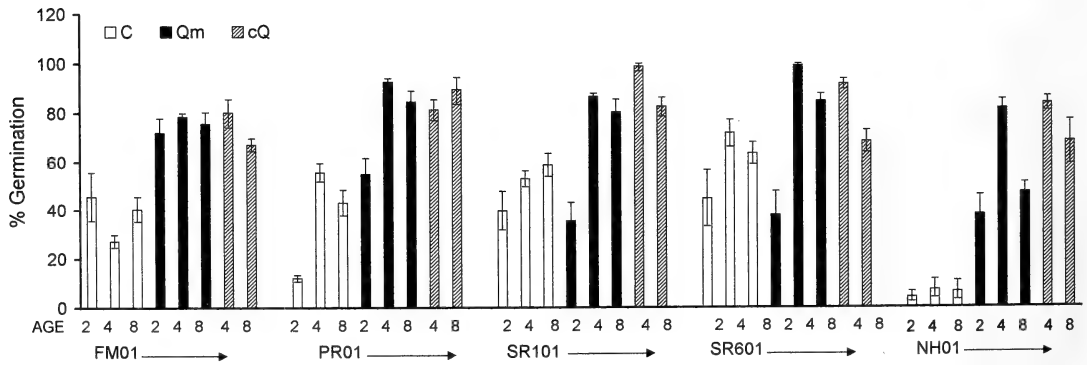


FIG. 6. Experiment 6 backtransformed germination data. Data are arranged by population, treatment, and seed age (in months) along the x-axis. Seeds aged 7.5 weeks are noted as "8". Data for liquid smoke followed by cold treatment (cQ) were compared with mQ-1 treatment in a separate analysis. Week 4 and week 8 cQ seeds were exposed to 4 weeks at 3.5°C and 2 weeks at 3°C, respectively. Error bars = 1 SD (n = 5).

could be more effective if applied before a cold treatment, but this was not tested. Exposure to 85°C for 10 minutes (H and SH) generally reduced germination of viable seeds, decreasing it to about a third of control values. Viability of heat-treated seeds also decreased by an average of 6%, stressing a need for further studies on heat sensitivity of this species.

We expect that seeds near the soil surface where temperatures are higher will be largely killed or inhibited by the heat of fire. In low intensity burns in chaparral, temperatures ranged from about 60°C at a depth of 7–8 cm, about 82°C at 2–3 cm, about 100°C at 1–2 cm deep, to over 180°C at the surface. Also, as fire intensity increased with increase in fuel load, temperatures deep into the seed bank became higher (Moreno and Oechel 1991). Higher fire intensities are known to deplete seed banks of other species (Odion 2000). Presumably, prescribed burning of grassland and relatively open California poppy habitats, with less above ground biomass than chaparral, will result in lower fire intensity and heat < 85°C at depths below 2 cm. Our testing at 85°C may adequately represent conditions of a low intensity fire in the upper 2 cm of dry soil where a high density of seeds is expected to occur.

Moist soil has higher thermoconductivity which can result in much higher temperatures to greater depths (DeBano et al. 1998). This has implications for the survival of seed banks of temperature sensitive species following spring burns over moist soil. In addition, Roche et al. (1998) found much higher germination and survival from smoke treated seedbanks when treated in the dry autumn before winter rains than when treated in winter or spring. Further studies are needed to determine the proportion of seeds killed at different burial depths over a range of fire soil temperatures and moisture levels.

*Cold treatment and incubation.* Many species require cold temperatures to break dormancy or for optimal germination of conditionally dormant seeds (Bewley and Black 1994; Baskin and Baskin 1998), and intra-species differences in response to chilling have been detected in other geographically variable species. For example, in *Artemisia tridentata* Nutt., which also germinates in winter, among-population differences were found in germination response to different temperatures, with the responses correlating to mean January temperature (Meyer et al. 1990; Meyer and Monsen 1992). In *E. californica*, populations differed in response to chilling, but it is too early to tell if response correlates with habitat.

We examined chilling under different moisture levels (dry, moist, wet) because cold winter temperatures in California (mid December–February) occur partly while the soil is still dry, and partly after the onset of winter rains. Furthermore, some species have higher seed germination after dry-cold

storage (Padgett et al. 1999). However, for California poppy, compared to no-cold controls, we found a slightly negative effect of wet-cold, no significant benefit of dry-cold, and only a weak effect of moist-cold treatment. Moist-cold resulted in higher germination than no-cold treatment in only six of 13 trials (Table 6). Two reviews of seed dormancy report dormant embryos generally need to be imbibed before they respond to chilling (Nikolaeva 1969; Baskin and Baskin 1998). It is unlikely that a chilling period longer than 4–8 wk would improve germination. In southern California, poppies germinate primarily in January and February, so seeds frequently receive a relatively short period of cold moist exposure, perhaps 2–8 wk, depending on location and onset of rains. In winter 2000, for example, native soils were dry into January in Riverside County, yet there was a spectacular bloom that spring.

The response of seeds to the various cold treatments was, in part, consistent with the dormancy behavior of a winter annual/perennial strategy. Many species in lowland Mediterranean climates germinate and grow in the cool winter rainy season between late fall and late winter. In some of these, prolonged warm summer temperatures or shelf storage can break dormancy while many have the ability to germinate at temperatures above about 5°C (Baskin and Baskin 1998). Instead of cold temperatures necessarily breaking dormancy, very cold temperatures can sometimes send seeds of winter annuals back into dormancy (Baskin and Baskin 1998) or increase degradation of viability (Priestley 1986). In our first two experiments with the lowest temperature cold treatment (2–4°C), dry cold did not cause a decrease in germination, but moist- and wet-cold treatments appeared to either increase dormancy of some wild seeds or increase degradation of viable seeds to the extent they lost the ability to germinate. This cold had no effect on domesticated seeds which germinated to nearly 100%. Dry smoke treatment applied before cold had an ameliorating effect on the lowering of germination (Exp. 2), but smoke treatments applied after cold did not. Cold-shock at 2°C actually decreased germination slightly or had no effect (Exp. 5), a result consistent with a “typical” winter annual strategy. Treatment at 3–3.5°C did not obviously depress or enhance germination (Exp. 6). Seeds exposed to cold treatments above 4°C began germination in the cold chamber and continued to germinate after moving to warmer incubation chambers (Exp. 3, 4). There was no consistent trend indicating which of the cold temperature treatments improved germination most. Treatment at 4–9°C (mostly 7°C) did not break dormancy in fire controls but did increase germination of smoke-treated seeds. Across experiments, germination appeared to improve under cooler incubation temperatures, especially once dormancy was broken with smoke. In addition, the two lower incubation temperatures (7.5 and 18/6°C

vs. 22/12°C) resulted in small significant increases in germination (Exp. 5). Lower temperatures are consistent with seed lab testing of California poppy at 15°C (Association of Official Seed Analysts 1981). The temperature range (2–4°C–22/12°C) under which perennial, domesticated poppies germinated to 100% was quite large, suggesting broad tolerances in the original source populations or selection for broad tolerances and loss of conditional dormancy under domestication. Overall, these results show that the effect of cold is subtle as well as population-specific. The results merit further investigation into optimal germination temperatures, how warm storage temperatures (higher than for shelf storage) affect dormancy break, and how effects vary among populations of different life-histories (annual vs. perennial) and from different climates.

Although California poppy has a small linear embryo, it does not appear to have the morphophysiological dormancy expected by Martin (1946). If there is such dormancy in California poppy, it is not general to all populations. Even in wild populations with dormant seeds, some seeds appeared to lack physiological dormancy. Extraordinarily high germination of domesticated seeds from commercial sources and naturalized garden plants even within two weeks of collection without pretreatment, may be due to lost genetic components important to germination cycles in natural populations. Most of the fresh seeds collected in 2001 became less dormant as they aged from 2 to 4 and ~8 months. There was some germination by two months suggesting seeds underwent some after-ripening by 2 months. Increased germination at 4 mo suggests seeds continued to mature in lab storage. For all but the Santa Barbara seeds, smoke treatment promoted higher seed germination than controls even at 2 mo, but was even more effective after 4 mo of aging for all populations. Further studies are required to reveal if embryos grow during dry storage or if their growth follows hydration with or without dormancy breaking smoke treatment. The ability of smoke to break dormancy in seeds less than 4 mo of age suggests that smoke from early summer fires may break dormancy prematurely, possibly making seeds vulnerable to germinating after summer rain if germination could occur at warm temperatures.

Because species with morphophysiological dormancy sometimes respond to moist-warm temperature followed by cold or by GA3 (Nikolaeva 1969; Hidayati et al. 2000), we exposed dormant, aged seeds of FM96 and NH98 to one week of warm-moist stratification at 28°C (A.M.M. and L.F. unpublished). We chose one week because in southern California's hot dry summer environment, soil dries out at most within a week of summer storms. Warm stratification did not improve germination over controls even when followed by GA3 (500ppm). GA3 treatment improved germination much less than liq-

uid smoke. We plan to test additional combinations of warm stratification followed by cold incubation treatments.

*Synergistic effects of smoke and cold.* We did find a weak synergistic effect of cold treatment in combination with smoke treatments for six populations in an overview of experiments in which smoke treatment was applied before cold treatment (Table 6). Under no-cold, there was consistently higher germination for liquid smoke than no-smoke controls in 15 of 15 trials; under moist-cold, liquid smoke resulted in even higher germination in seven of nine trials (Table 6, Exp. 2–5). Similarly, under no-cold, dry smoke treatment resulted in higher germination than no-smoke controls in 10 of 13 trials; under moist-cold, dry-smoke resulted in even higher germination in 10 of 13 trials. This synergism suggests smoke is triggering a growth sequence that must occur before cold temperatures can succeed in promoting germination and may, in part, be substituting for other environmental cues that would normally occur before cold treatment (e.g., warm summer temperatures or exogenous chemicals in the soil).

*Seed age.* Interestingly, young seeds had lower seed dormancy than aged seeds from the same populations, and dormancy was easier to break than in aged seeds. In young seeds, dry smoke increased germination over the controls, and liquid smoke produced the highest germination of any treatment (62–95% in young seeds vs. 0–70% in aged seeds). Viability dropped no more than 6% between young and aged collections from the same sites (viability confirmed with TZ and checked with fluoroscein diacetate methods, unpubl. after Windholm 1972), indicating that older seeds entered a secondary dormancy during prolonged shelf storage, or that seeds experienced deterioration in germinability that cannot be detected with chemical viability tests. Additional cues may be required to break any secondary dormancy. The ability to enter secondary dormancy is important to seasonal cycling of dormancy, the building of a seed bank, and presence of a bet-hedging strategy in unpredictable environments. This may be especially important to seeds that germinate in dark so that the seed bank is not exhausted in any particular year.

*Variation within and among populations.* Even though smoke alone or with cold succeeded in increasing germination across populations, populations differed substantially in response to those treatments and in baseline dormancy of untreated, shelf-stored seeds. Populations also differed in response to wet or dry smoke treatments, often in association with annuality or perenniality (Exp. 4). Furthermore, in all wild populations and treatments a fraction of the viable seeds did not germinate. This is important for several reasons: 1) we have not identified a general natural cue that promotes germination of young seeds enmasse in the absence

of fire, or of aged seeds enmasse with or without fire; 2) there are differences among seeds within populations for dormancy and dormancy breaking requirements; and 3) if the variation in response is heritable it can be selected and thus the observed variation in response among populations may be the result of adaptation to local conditions and may be linked to different life-history strategies (Cook 1962; Young and Augspurger 1991). Variation within populations, including changes with seed age, may provide a good bet-hedging strategy.

Clearly, the domesticated (Dom and RIV) populations of California poppy with their non-dormant seeds were very different from all wild populations in our study. Interestingly, some perennial populations from coastal northern California also have no seed dormancy (Cook 1962; Montalvo personal observation, e.g., RM01). Large differences among wild-collected populations, and between wild and the domesticated populations, show the importance of noting seed source and population traits when doing research or restoration with this species. Our results indicate that results of seed dormancy experiments from one or two populations cannot be generalized correctly to the species level. Research on a range of wild populations which have different levels of seed dormancy, including perennial populations with non-dormant seeds needs to be done before any generalizations can be made about light inhibition of germination and requirements for germination in this species.

*In pursuit of unknown cues.* We have not discovered how to break dormancy without smoking seeds. Given that many California poppy seeds germinate in nature in the absence of fire, future work should explore the combined effects of seed burial and seasonal changes in temperature on seed germination, with and without smoke. In several Australian species, prolonged seed burial was found to affect the seed coat by increasing permeability to water and seed coat breakage in ways that facilitated germination (Tieu and Egerton-Warbuton 2000). In addition, Roche et al. (1997a) found a synergistic effect of lengthy seed burial followed by smoke addition on germination of 60% of over 100 Australian species tested. Smoke treatment by itself approximately doubled germination of seeds, but smoke treatment combined with soil storage quadrupled germination. Seed burial was also found to be important to germination of *Dendromecon rigida* Benth., a fire following species in the Papaveraceae (Keeley and Fotheringham 1998b) that is closely related to the genus *Eschscholzia*. It is possible that some dormant poppy seeds require a combination of seed burial and changing temperatures before they can successfully germinate. Although exposure to warm summer temperatures breaks dormancy in many winter annuals (Baskin and Baskin 1998), in a recent seed burial study where the soil was dry, as is natural in this region,

we found that exposure to natural summer and early fall temperatures (July–mid November) did not notably improve germination relative to shelf-stored controls (A. Montalvo and C. Koehler unpublished data).

*Implications for conservation and restoration.* Given the beneficial effect of smoke treatments on California poppy germination, prescribed fire might prove useful for poppy management as long as heat does not penetrate into the seed bank too deeply. Liquid smoke treatment of the seed bank may simulate the beneficial effects of fire when prescribed burning is not feasible or when heat might unduly affect viability of poppy or other native species. On a cautionary note, evaluation of the differential effects of smoke on other species, both native and exotic, is warranted before using smoke and/or fire as a management tool. Seeds of exotic and native species may differ in response to smoke treatment and changes in seed coat chemistry may be irreversible (Roche et al. 1998). If smoke facilitates a non-reversible breaking of seed dormancy for a large fraction of the seed bank, then effects of frequent or even occasional burning could last more than one season and could disrupt the selective value of dormancy. The seedbank could be depleted if seeds germinate under conditions detrimental to successful establishment. It is important to weigh the consequences of such negative direct effects of repeated burning on the seed bank, against the beneficial effects of killing competitors, or perceived benefit of managing for large flowering displays.

Our results can help to develop regionally adapted populations of California poppy for restoration and revegetation projects in southern California, which have in the past met with mixed success. In xeric, non-irrigated locations where native poppies tend to have largely dormant seeds, plantings of domesticated seeds can die out within a few years (A. Montalvo personal observation). Most commercially available poppy seeds are non-dormant, perennial, and have resulted from many generations of seed increase, a practice that selects against seed dormancy. The seed industry has avoided dealing in native, dormant seeded populations, in part because it is difficult to break their seed dormancy (Victor Schaff, S&S Seeds personal communication). In the future, the seed industry could smoke-treat dormant native poppy seeds before planting to avoid selecting against seed dormancy. Given the evidence for locally adaptive differences and home site advantage in many other plant species (for review see Langlet 1971; Montalvo and Ellstrand 2000), and the sometimes adverse effects of hybridization among genetically differentiated populations (Millar and Libby 1989; Knapp and Rice 1994; Montalvo et al. 1997, Montalvo and Ellstrand 2001), the use of local poppy seeds for restoration and reseeded would likely increase the long-term success of planted populations.



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## TEMPERATURE LIMITATIONS FOR CULTIVATION OF EDIBLE CACTI IN CALIFORNIA

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### ABSTRACT

*Hylocereus undatus* (a hemiepiphyte) and *Opuntia ficus-indica* (“prickly pear”) are cultivated worldwide as specialty fruit and vegetable crops, so the role of temperature in determining regions suitable for commercial growth of these cacti was investigated for California, the leading agricultural state in the United States. Air temperatures below  $-2.5^{\circ}\text{C}$  and above  $45^{\circ}\text{C}$  are lethal for *H. undatus* compared with below  $-10^{\circ}\text{C}$  and above  $65^{\circ}\text{C}$  for *O. ficus-indica*, demonstrating the latter’s greater tolerance of extreme temperatures. Mean nighttime air temperatures influence net  $\text{CO}_2$  uptake for these Crassulacean acid metabolism species, optimal uptake occurring at  $20^{\circ}\text{C}$  for *H. undatus* and at  $14^{\circ}\text{C}$  for *O. ficus-indica*. Extreme air temperatures over a 30-year period for 326 weather stations and mean nighttime temperatures for 259 stations were mapped to identify where these species could be cultivated. Only 2% of the state’s total area avoided temperatures lethal to *H. undatus*, mostly along the southern coast. In contrast, 36% of the state’s area was possible for *O. ficus-indica*, exclusion occurring in mountainous regions. A Temperature Index (net  $\text{CO}_2$  uptake over 24-hour periods at a particular temperature divided by uptake at the optimal temperature) was also utilized to evaluate a region’s suitability for growing these cacti. The Temperature Index was below 0.7 for 59% of the weather stations for *H. undatus* but for only 16% for *O. ficus-indica*. In the regions where lethal extreme temperatures did not occur, the Temperature Index averaged more than 0.8 for both species. Use of a Temperature Index based on net  $\text{CO}_2$  uptake together with extreme temperature events can help evaluate regions for cultivating cacti with edible fruits or other new crops.

Key Words:  $\text{CO}_2$  uptake, Crassulacean acid metabolism, fruit, *Hylocereus undatus*, *Opuntia ficus-indica*.

As a result of its geology, topography, and climate, California is the most biodiverse state in the United States, having nearly 6000 native species of vascular plants (Hickman 1993). Such variety also permits the production of about 350 agricultural commodities that generate \$30 billion in revenue per year, more than for any other state, such commodities being responsible for 10% of the jobs in California (California Department of Food and Agriculture 2001). Much of the agricultural economy derives from intensively managed specialty crops—e.g., minor crops such as grapes, tomatoes, strawberries, lettuce, and flowers generate about 20% of the agricultural sector’s annual revenue (California Department of Food and Agriculture 2001). In this regard, considerable interest exists among both government officials and also producers to develop new specialty crops, such as the cacti with edible fruits considered here.

Given their potentially high productivity and tolerance of high temperatures (Nobel 1988), cacti have become important crops in arid and semiarid regions worldwide (Barbera 1995). The prickly pear cactus *Opuntia ficus-indica* (L.) Miller is cultivated on over one million hectares in more than 30 countries primarily for fodder but also as a fruit

crop (“cactus pears”) and on a limited scale as a vegetable crop (“nopalitos”; Nobel 2000). Second in importance among edible cacti are hemiepiphytes in the genera *Hylocereus* and *Selenicereus*, whose fruits are commonly referred to as “pitahayas,” which are cultivated in 20 countries, with particularly noteworthy success in Southeast Asia (Nerd et al. 2002; Nobel and De la Barrera 2002). Cacti have been cultivated in California since the eighteenth century, when *O. ficus-indica* was planted around the Spanish missions along the coast for its fruit and its mucilage, which was utilized as a binding material for adobe bricks (McLeod 1975). In the early 1900s, Luther Burbank, who pioneered several specialty crops, developed a “spineless” variety of *O. ficus-indica* (Savio 1989). The D’Arrigo Brothers have plantations of spineless *O. ficus-indica* in the Santa Clara Valley (also known as the Salinas Valley) near Gilroy that were established in the 1920s for fruit (Curtis 1977), and various companies in southern California are currently exploring the pitahaya market (Savio 1989; Valdivia 2000; P.S. Nobel personal observation).

Most gas exchange for cacti occurs at night when air temperatures are lower than during the daytime, a characteristic of the Crassulacean acid metabolism (CAM) photosynthetic pathway. This physiological strategy, which has evolved for species in over 30 vascular plant families, reduces transpira-

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tional water loss (Nobel 1999; Taiz and Zeiger 2002). Optimal nocturnal air temperatures for net  $\text{CO}_2$  uptake by CAM plants are generally from 10 to 20°C (Nobel 1988). Extreme temperatures limit  $\text{CO}_2$  uptake and also can damage cacti, with episodic freezing temperatures generally being more limiting to plant distribution than high temperatures. For instance, based on the uptake of a vital stain into the central vacuoles, the photosynthetic cells (chlorenchyma) of *O. ficus-indica* have 50% mortality ( $\text{LT}_{50}$ ) at the extremely high temperature of 62.4°C for plants kept at day/night air temperatures of 40/30°C and at 66.6°C for plants kept at 50/40°C, indicating that *O. ficus-indica* has a high-temperature acclimation (hardening) of 4.2°C per 10°C increase in air temperature (Nobel 1988). The  $\text{LT}_{50}$  for low-temperature tolerance of *O. ficus-indica* is -7.7°C for plants kept at day/night air temperatures of 20/10°C, decreasing to -8.8°C for plants kept at 10/0°C, indicating a low-temperature acclimation of 1.1°C for a temperature decrease of 10°C (Nobel 1988). *Hylocereus undatus* (Haworth) Britton & Rose, which is native to neotropical forests (Britton and Rose 1963; Backeberg 1966; Barthlott and Hunt 1993) where temperatures tend to be warm and vary little over the course of a year (Croat 1978; Lüttge 1997), shows a high-temperature acclimation of only 1.4°C per 10°C increment in air temperature, as  $\text{LT}_{50}$  occurs at 54.0°C for plants kept at day/night air temperatures of 25/15°C and at 55.4°C for plants at 35/25°C; furthermore, plants kept at 40/30°C develop stem tissue necrosis, leading to death after 19 weeks (Nobel and De la Barrera 2002). Because the responses of *H. undatus* to freezing temperatures have not been reported, one of the objectives of the present research was to determine its low-temperature tolerance and its low-temperature acclimation.

An Environmental Productivity Index (EPI), which can help to evaluate the feasibility for expanding the area of cultivation of crops such as cacti, indicates the primary influence of water, temperature, and light on net  $\text{CO}_2$  uptake and hence biomass productivity of plants (Nobel 1988, 1999). EPI is defined as the Water Index  $\times$  the Temperature Index  $\times$  the PPF Index (PPF refers to the photosynthetic photon flux, composed of wavelengths of light from 400 to 700 nm), where each component index ranges from 0.00, when that environmental factor eliminates net  $\text{CO}_2$  uptake, to 1.00, when that factor is optimal for net  $\text{CO}_2$  uptake (Nobel 1988). EPI ignores secondary interactions, such as the different response to PPF when temperature is limiting, but in any case net  $\text{CO}_2$  uptake is generally low under such conditions. The individual indices are determined in the laboratory under controlled conditions over 24-hour periods by varying the environmental parameter to be studied, while keeping the other factors constant at optimal values. EPI can then be calculated under field environmental conditions, as has been done to predict quanti-

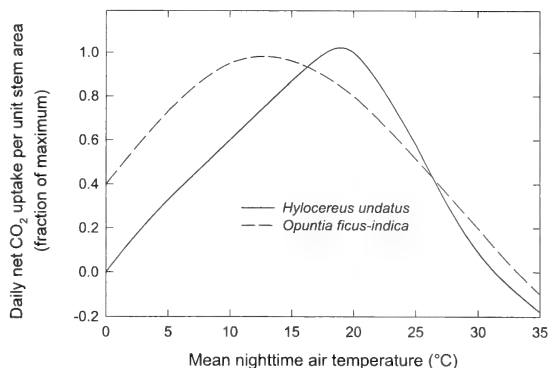


FIG. 1. Responses of total daily net  $\text{CO}_2$  uptake by *Hylocereus undatus* and *Opuntia ficus-indica* to mean nighttime air temperatures. Plants were maintained for 7 to 14 days at a particular temperature before measurement. Data for *H. undatus* are from Raveh et al. (1995) and Nobel and De la Barrera (2002) and for *O. ficus-indica* are from Nobel (1988) and Nobel and Bobich (2002).

tatively the growth of *Agave deserti* along an elevational gradient (Nobel 1984) and to establish new plantations of *O. ficus-indica* in Chile (P. S. Nobel personal observation). For agricultural purposes, the Water Index can be increased to 1.0 by irrigation, and the PPF Index can be manipulated by varying the spacing between plants. However, it is difficult to control temperatures in the field. Determining the Temperature Index may therefore help producers decide the suitability of a particular region for growing a certain crop. In this regard, net  $\text{CO}_2$  uptake is optimal at a mean nighttime temperature of 20°C for *H. undatus* and 14°C for *O. ficus-indica* (Fig. 1). Also, *H. undatus* has a narrower temperature range than does *O. ficus-indica* within which the Temperature Index is above 0.5 (9 to 26°C versus 2 to 26°C) and above 0.8 (14 to 23°C versus 6 to 20°C). The present research uses the previously measured Temperature Indices for *H. undatus* and *O. ficus-indica* (Fig. 1), the low and the high temperature tolerances for both species, and climatic data to evaluate potential regions for their cultivation in California. This approach used for cacti here can also serve as a model for assessing the cultivation potential of other plant species.

#### MATERIALS AND METHODS

**Temperature tolerances.** The low-temperature tolerance has already been determined for *Opuntia ficus-indica*, as have the high-temperature tolerance for it and *Hylocereus undatus* (Nobel 1982, 1988; Nobel and De la Barrera 2002), using the vacuolar uptake of neutral red (3-amino-7-dimethylamino-2-methylphenazine hydrochloride) following exposure for 60 min to a particular extreme temperature (Onwueme 1979; Didden-Zopf and Nobel 1982; Nobel et al. 1995). Hence, the low-temperature tolerance of *H. undatus* was similarly

determined here using the neutral red assay. For this purpose, five plants approximately 45 cm in shoot length were obtained from the Cactus Trading Company (Jamul, CA). They were grown in each of two Conviron E-15 environmental chambers (Controlled Environments, Pembina, ND) with day/night air temperatures of 20/10°C or 30/20°C for 4 weeks with weekly application of 0.2-strength Hoagland's solution supplemented with micronutrients and a total daily PPF of 16 mol m<sup>-2</sup> day<sup>-1</sup>, environmental conditions that are near the optimal for *H. undatus* (Raveh et al. 1995; Nobel and De la Barrera 2002).

Low temperatures at 1 to 2°C intervals decreasing from 4°C were obtained in an ULT-80 ultra-low-temperature freezer (Rheem Manufacturing, West Columbia, SC). Approximately 1.5 g of stems were removed with a scalpel, placed in contact with a copper-constantan thermocouple 0.51 mm in diameter, and wrapped in aluminum foil to prevent desiccation; the samples were then cooled at 5°C hr<sup>-1</sup>, similar to stem cooling rates observed in the field (Nobel 1988; Nobel et al. 1995). After exposure to a particular temperature for 60 min, the samples were sliced into sections approximately 700 µm thick using razor blades and then placed in 0.2% (w/w) neutral red for 90 min for stain uptake, which occurs for the vacuoles of living cells only and indicates membrane integrity (Onwueme 1979; Nobel et al. 1995). The tissue samples were then placed for 10 min in 0.25 M potassium phosphate buffer (pH 7.8) at 25°C followed by 24 hours at 6°C in distilled water to help remove excess stain and hence to sharpen the images, after which approximately 130 intact cells per sample were examined at 100× using a BH-2 phase-contrast microscope (Olympus, Lake Success, NY) to check for stained (living) versus unstained cells. The low temperature treatment that halved stain uptake from the maximum occurring at 4°C (LT<sub>50</sub>), a reliable test for predicting eventual tissue necrosis (Didden-Zopf and Nobel 1982; Smith et al. 1984; Nobel et al. 1995), was determined graphically under each condition. Low-temperature acclimation was analyzed by comparing LT<sub>50</sub> for plants at day/night air temperatures of 20/10°C versus 30/20°C using an unpaired Student t-test.

**Extreme temperature limitation.** For cacti in nature as well as under cultivation, infrequent freezing episodes can be severely limiting (Steenbergh and Lowe 1976; Russell and Felker 1987; Nobel 1988). Moreover, fruit production by *H. undatus* and *O. ficus-indica* can occur two years after the establishment of a plantation, but approximately 10 years may be necessary to obtain optimal yields and an even longer period for appropriate return on the initial investment (Mizrahi and Nerd 1999; Inglese et al. 2000; Nerd et al. 2002). Also, the fruiting potential of *O. ficus-indica* tends to decrease after 25 to 30 years (Inglese et al. 2002). Thus,

instead of using annual minimum temperatures, the lowest air temperatures recorded between 1961 and 1990 (the most recent period summarized with climate normals) at 326 California weather stations were obtained from the Climate Atlas of the Contiguous United States (National Climatic Data Center 1995). Similarly, the highest air temperatures were obtained for the 318 weather stations with suitable records for the same period. The temperatures were converted from Fahrenheit to Celsius and then ranked in 2.5°C intervals for low-temperature extremes or 5°C intervals for high-temperature extremes. In addition, weather station data were interpolated, correcting for elevation using a lapse rate of 6°C per km (Nobel 1999), to identify the areas with record minimum temperatures below -10°C or above -2.5°C as well as record maximum temperatures above 45°C over the 30-year period (1961–1990). The resulting low-temperature and high-temperature maps were created in ArcView 3.1 (ESRI, Redlands, CA).

**Temperature Index.** Daily minimum temperatures averaged over each month for the California weather stations from 1961 to 1990 and then averaged over the 30 years were also obtained from the Climate Atlas of the Contiguous United States (National Climatic Data Center 1995). Nighttime mean air temperatures were estimated by adding 3°C to the average minimum temperature (Nobel 1988) recorded at each of the 259 weather stations with sufficient records. The Temperature Index for total daily net CO<sub>2</sub> uptake per unit stem area for *H. undatus* and *O. ficus-indica* was then determined for each month using the known temperature responses for these two species (Fig. 1). The twelve monthly values were averaged to obtain an annual Temperature Index for each weather station and maps were created in ArcView 3.1.

## RESULTS

**Low-temperature tolerance for *Hylocereus undatus*.** Neutral red accumulation in chlorenchyma cells of *Hylocereus undatus* decreased as the treatment temperature was lowered below 0°C (Fig. 2). For *H. undatus* growing at day/night air temperatures of 30/20°C, the percentage of cells taking up the vital stain was halved (LT<sub>50</sub>) at  $-1.31 \pm 0.04^\circ\text{C}$ . The LT<sub>50</sub> for *H. undatus* acclimated to day/night air temperatures of 20/10°C was  $-1.55 \pm 0.07^\circ\text{C}$ . This species thus displayed a small, yet significant, low-temperature acclimation (hardening) of  $0.24 \pm 0.08^\circ\text{C}$  per 10°C decrease in temperature ( $t = 2.98$ ,  $P < 0.01$ ,  $df = 8$ ).

**Extreme temperature limitations.** During the 30-year period considered (1961–1990), 40% of the 326 weather stations had temperatures below -10°C, corresponding to 64% of the area of California, mainly in regions at high elevations in the Sierra Nevada, Coast and Diablo ranges, and the San Bernardino Mountains, as well as in northern

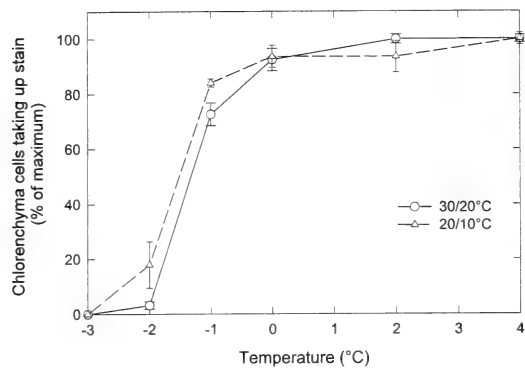


FIG. 2. Influence of day/night air temperatures of 20/10°C and 30/20°C on the low-temperature tolerance of *H. undatus*. Uptake of neutral red was determined for pieces of chlorenchyma incubated at a particular treatment temperature for 60 min. Data are means  $\pm$  SE ( $n = 5$  plants).

California (Fig. 3A). Regions with extreme minimum temperatures from  $-5$  to  $-10^{\circ}\text{C}$  (49% of the stations) are concentrated along the coast, through the Central Valley, and in southern California. Regions that were never below  $-5^{\circ}\text{C}$  (11% of the stations) are largely restricted to thin coastal regions in the San Francisco Bay area, the Channel Islands, and in southern California from Ventura to San Diego counties, in addition to lower inland elevations in southern California. Regions with extreme minimum temperatures above  $-2.5^{\circ}\text{C}$  (7% of the stations), representing only 2% of the state's area, are located along the coast in Ventura, Los Angeles, Orange, and San Diego counties plus one station in the San Francisco Bay area (Fig. 3B). Only one station (at the University of California, Los Angeles) remained above  $0^{\circ}\text{C}$  during the period considered (1961–1990).

During the same 30-year period, five weather stations had maximum temperatures above  $50^{\circ}\text{C}$

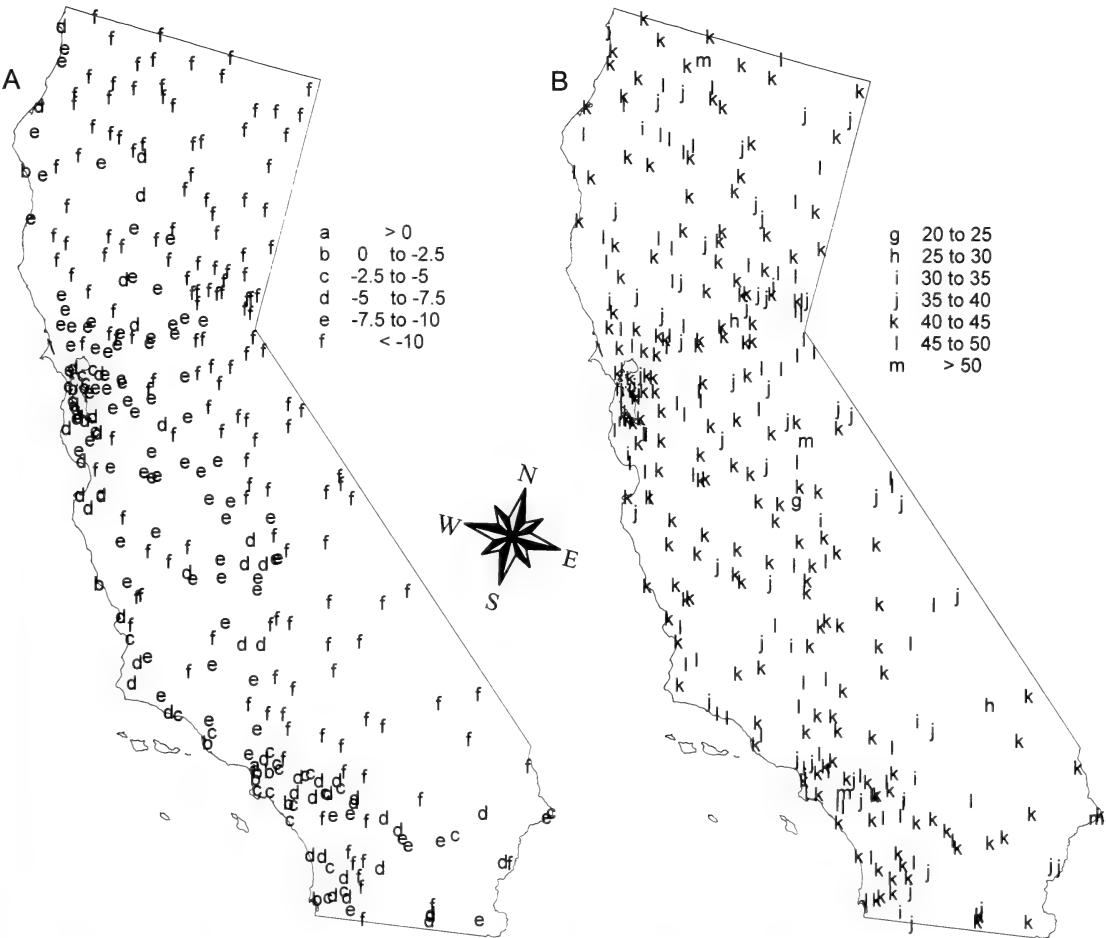


FIG. 3. Temperature extremes at California weather stations from 1961–1990: (A) record minimum temperatures and (B) record maximum temperatures. Letters indicate specific ranges of extreme temperatures, e.g., c corresponds to a record minimum temperature between  $-2.5^{\circ}\text{C}$  and  $-5^{\circ}\text{C}$ .

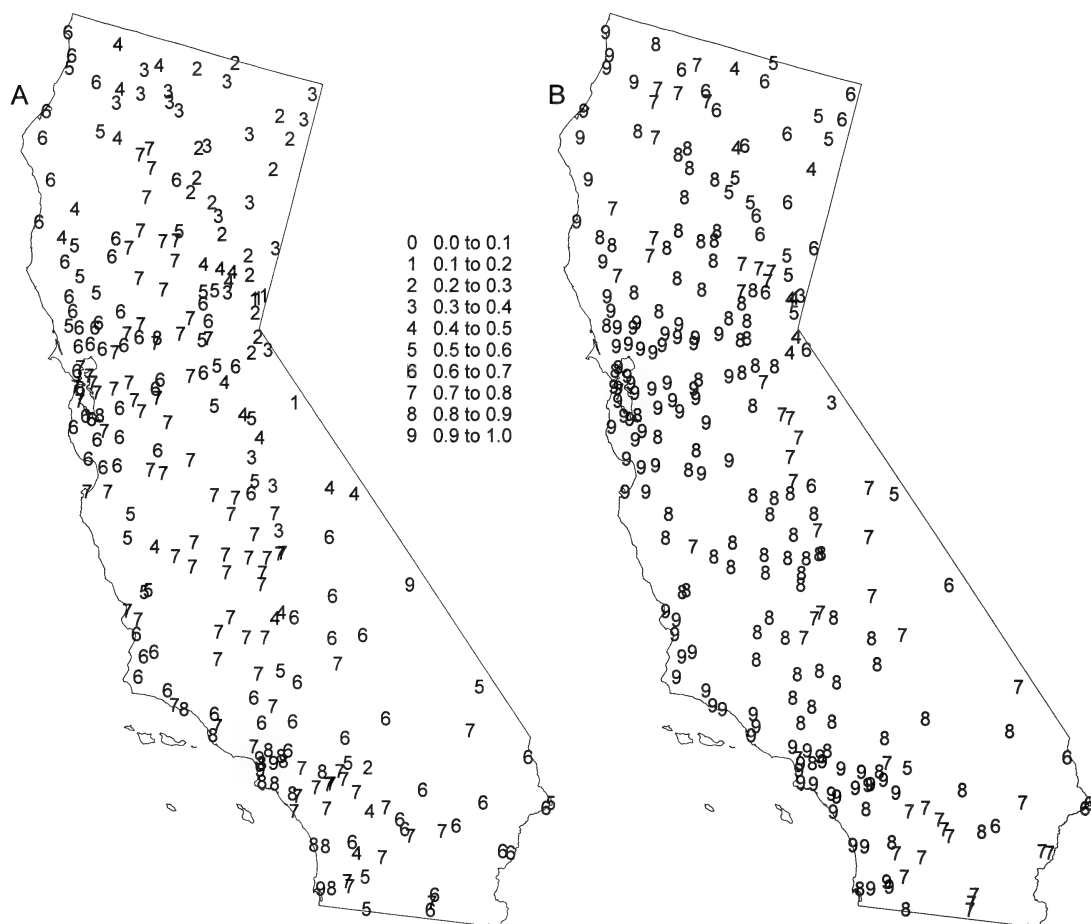


FIG. 4. Annual Temperature Index values at California weather stations averaged over 30 years (1961–1990) for (A) *H. undatus* and (B) *O. ficus-indica*. Each number represents the influence of temperature on the fraction of maximal total daily net CO<sub>2</sub> uptake averaged over the year, as calculated from monthly mean nighttime air temperatures, for each weather station. Numbers indicate specific ranges of the annual Temperature Index, e.g., 7 corresponds to 0.7 to 0.8.

(1.6% of the 318 stations), with the hottest site (53°C) in Death Valley (Fig. 3B). Maximum temperatures from 45 to 50°C occurred at 26% of the weather stations, concentrated at lower elevations in the Mojave Desert and Death Valley, along the Central Valley, and in inland southern California. Approximately 40% of the state's area had temperatures above 45°C during the period considered. Regions with maximum temperatures from 40 to 45°C for the 30-year period considered (53% of the stations) are situated at higher elevations in northern California, in the Central Valley, and along the coast from the San Francisco Bay area through San Diego County. Only 20% of the stations, distributed in coastal regions or at high mountain elevations, recorded maximum temperatures below 40°C (Fig. 3B).

**Temperature Index.** For *H. undatus*, the annual Temperature Index (TI) was below 0.5 for 23% of the 259 weather stations, mostly those at high elevations, especially in northern and inland California (Fig. 4A). An annual TI of 0.5 to 0.7 occurred for 36% of the stations, most occurring in the Central and Imperial valleys. An annual TI from 0.7 to 0.8 was restricted to Sacramento, the San Francisco Bay area, and the southern California coast (33% of the stations; Fig. 4A). A TI of 0.8 to 0.9 was found only in Los Angeles, Orange, and San Diego counties as well as in Death Valley (8% of the stations).

Compared with *H. undatus*, the annual TI tended to be higher for *Opuntia ficus-indica*, only 4% of the weather stations having annual values below 0.5 (Fig. 4B). An annual TI of 0.5 to 0.7 occurred for

12% of the stations, mostly in inland regions, especially for northeastern California. Moderately high TI, from 0.7 to 0.8 (18% of the stations) and from 0.8 to 0.9 (32% of the stations), were located throughout California, except at high elevations in the Sierra Nevada. Annual TI values above 0.9 for *O. ficus-indica* occurred along the coast from the Oregon border south to Ventura County as well as in various inland regions, such as in the San Francisco Bay area and the Los Angeles basin (34% of the stations; Fig. 4B).

## DISCUSSION

Twenty-three species of cacti have been examined for tolerance to extreme temperatures (Nobel 1982, 1988; Smith et al. 1984), which are important in determining natural distributions and potential regions for cultivation. The least freezing tolerant of these species, *Opuntia ramosissima*, is native to the deserts of the southwestern United States and northern Mexico and has an  $LT_{50}$  (temperature that kills half of the cells compared with the control) of  $-4.4^{\circ}\text{C}$  when maintained at day/night air temperatures of  $10/0^{\circ}\text{C}$  (Nobel 1982). *Hylocereus undatus* was even less freezing tolerant, with an  $LT_{50}$  of  $-1.6^{\circ}\text{C}$  when maintained at  $20/10^{\circ}\text{C}$ . Taking into consideration its relatively small low-temperature acclimation of  $0.2^{\circ}\text{C}$  per  $10^{\circ}\text{C}$  decrease in air temperature observed here, the  $LT_{50}$  for *H. undatus* is only  $-1.8^{\circ}\text{C}$  at  $10/0^{\circ}\text{C}$ , indicating that it is extremely sensitive to freezing temperatures. In addition, *H. undatus* is not as tolerant of high temperatures as are the other cactus species examined (Nobel 1988) and also exhibits little high-temperature acclimation (Nobel and De la Barrera 2002). Indeed, acclimation is the key to tolerating extreme temperatures, and only one cactus species (*Ferocactus covillei*) has less low-temperature acclimation and none has less high-temperature acclimation than does *H. undatus* (Nobel 1988). In this regard, *H. undatus* is native to neotropical forests with moderate and rather stable temperatures (Britton and Rose 1963; Backeberg 1966; Croat 1978; Barthlott and Hunt 1993; Lüttge 1997) and apparently is not genetically or physiologically capable of appreciable acclimation to low or to high temperatures, although further studies are necessary to understand its intraspecific variation.

$LT_{50}$  is used for its ease of measurement and because it is often the temperature where stem damage becomes visible, although cacti generally do not die until the cellular uptake of a vital stain is reduced to zero. As assessed by neutral red staining, stem death of most cacti occurs approximately  $4^{\circ}\text{C}$  below the low-temperature  $LT_{50}$  and  $4^{\circ}\text{C}$  above the high-temperature  $LT_{50}$  (Nobel et al. 1986; Nobel 1988). Moreover,  $LT_{50}$  refers to tissue temperatures when damage occurs, not air temperatures, which can differ significantly. On clear nights, temperatures of cactus stems can be a few degrees Celsius

below air temperature due to transpirational cooling and especially net heat loss by infrared (longwave) radiation (Nobel 1988, 1999). Indeed, radiation frosts, when the tissue achieves freezing temperatures with air temperatures above  $0^{\circ}\text{C}$ , are a severe agricultural problem in California, especially for the citrus industry (Pehrson 1984), and affect the suitability of a site for cactus cultivation. Freezing temperatures can cause extracellular ice crystal formation in cacti, which draws water out of the cells and can lead to irreversible damage (Burke et al. 1976; Nobel 1982, 1988). For regions that experience infrequent damaging or even lethal low temperatures, freeze-protection methods, such as shade cloth, heaters, and overhead irrigation, can mitigate freezing damage to perennial plants such as *H. undatus* and *O. ficus-indica* (Pehrson 1984; Perry 1998).

Differences between air and tissue temperatures can be even larger during the day than at night, depending on stem orientation relative to solar irradiation and stem massiveness (Nobel 1988). Tissue temperatures of the relatively thin stems of *H. undatus* are not expected to rise more than 1 to  $2^{\circ}\text{C}$  above air temperature, especially in its typically shaded habitat (Nobel and De la Barrera 2002). In contrast, stem temperatures for *O. ficus-indica* can be more than  $15^{\circ}\text{C}$  above air temperatures (Wallace and Clum 1938; Konis 1950). Extremely high temperatures can denature proteins, degrade cell membranes, and disrupt metabolism in general (Nobel 1988; Srinivasan et al. 1996; Taiz and Zeiger 2002). For *H. undatus*, daytime temperatures of  $45^{\circ}\text{C}$  can reduce flower and hence fruit production (Mizrahi and Nerd 1999). Shade cloth has been used to ameliorate the effects of high temperatures (and high PPF) on *H. undatus* growing in Israel (Raveh et al. 1998). In contrast, stems of *O. ficus-indica* usually are not damaged until air temperatures exceed  $65^{\circ}\text{C}$  and it can even tolerate 60 min at  $70^{\circ}\text{C}$  (Nobel et al. 1986; Nobel 1988), so high temperatures should not be a limiting factor for cultivation of this cactus in California.

*Hylocereus undatus* can be grown in regions with extreme temperatures above  $-2.5^{\circ}\text{C}$  and below  $45^{\circ}\text{C}$  (Fig. 5A), which occur for only 2% of the state's area. On the other hand, *O. ficus-indica* is excluded only from regions of California where the minimum temperature is below  $-10^{\circ}\text{C}$  (Fig. 5B) and can be grown in 36% of the state's area. The climate of California, which renders most of the state too cold for maximal net  $\text{CO}_2$  uptake by *H. undatus*, resulted in a lower annual Temperature Index (TI) for it, averaging 0.57 throughout the state compared to 0.82 for *O. ficus-indica*. The lower average annual TI for *H. undatus* reflects both its relatively high optimal mean nighttime temperature for net  $\text{CO}_2$  uptake and also the more rapid decrease in net  $\text{CO}_2$  uptake above and below the optimal value than is the case for *O. ficus-indica*. In the regions where the cacti can be cultivated be-

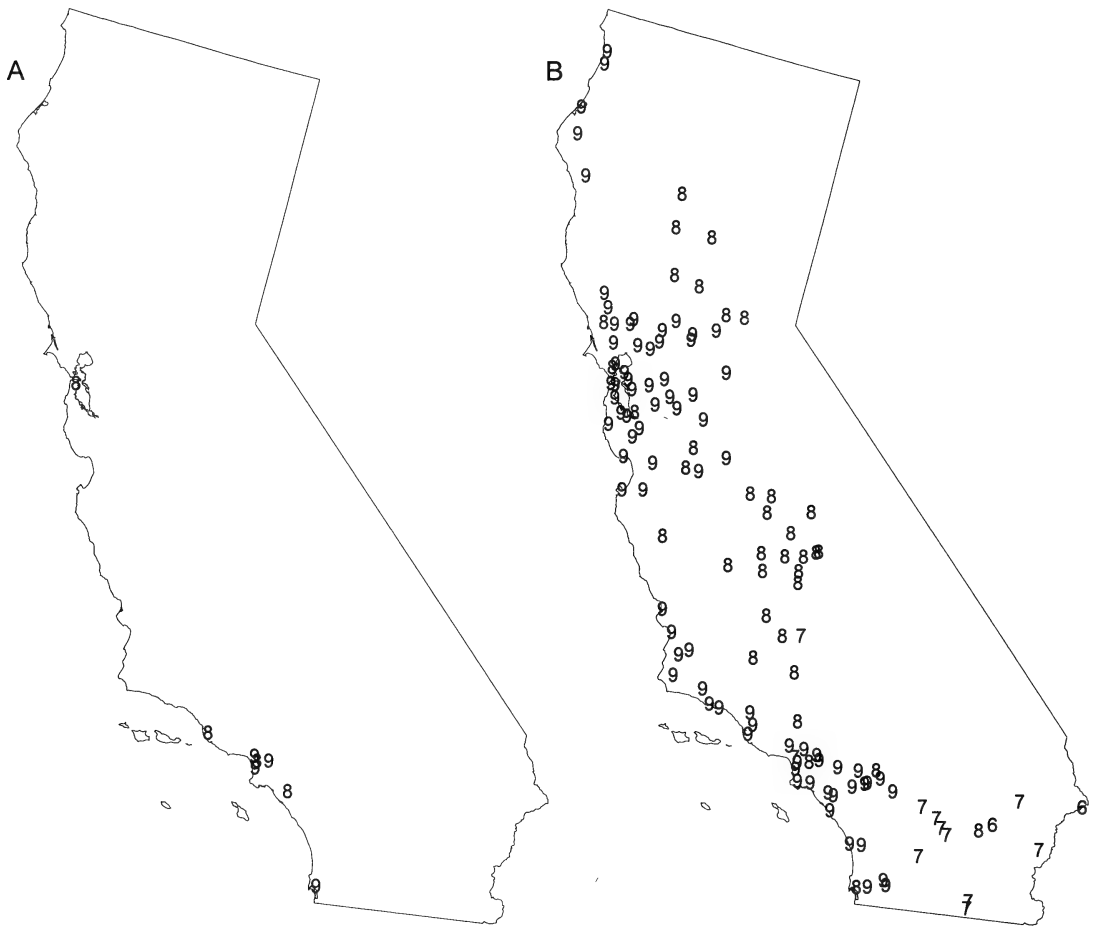


FIG. 5. Annual Temperature Index values (from Fig. 4) for the weather stations with extreme temperatures within the tolerable ranges for (A) *H. undatus* (extreme temperatures between  $-2.5^{\circ}\text{C}$  and  $45^{\circ}\text{C}$ ) and (B) *O. ficus-indica* (minimum temperature of  $-10^{\circ}\text{C}$  and no maximum temperature).

cause of lack of lethal extreme temperatures (Fig. 5), the annual TI averages 0.83 for *H. undatus* and 0.90 for *O. ficus-indica*, both high values, indicating that the nighttime temperatures for regions within the extreme temperature limits are conducive to substantial net  $\text{CO}_2$  uptake by these two species. The similarly high annual TI estimated for *O. ficus-indica* in areas suitable for cultivation (and in the entire state) reflect the wide range of nighttime temperatures at which this species can be grown successfully. Nevertheless, the exclusion of 64% of California's area indicates that even single extreme low-temperature events can greatly damage plantations of *O. ficus-indica* (Russell and Felker 1987; Nobel 1988). Frost damage can be avoided with appropriate agricultural practices (Pehrson 1984; Perry 1998) or by the utilization of cold-tolerant cultivars of *Opuntia*, a genus with considerable genetic diversity as well as a long history of agricul-

tural selection (Russell and Felker 1987; Parish and Felker 1997; Casas and Barbera 2002).

The Temperature Index is the least manageable of the three components of the Environmental Productivity Index (EPI) in an agricultural setting, which is the reason for its consideration in the present study. The relationship between EPI, a predictor of net  $\text{CO}_2$  uptake, and fruit production has not been investigated for *H. undatus* or *O. ficus-indica*, but EPI closely predicts leaf production for *Agave tequilana* (Nobel and Valenzuela 1987) and cladode production for *O. ficus-indica* (Nobel 1988) under cultivation. Besides the present focus on fruit crops and the use of young cladodes of *O. ficus-indica* as a vegetable, most cultivation of cacti worldwide is dedicated to fodder production (Nobel 2000), due to ease of management without irrigation or fertilizer application and an acceptable protein content of 5 to 8% on a dry mass basis (Nobel 1988; Pi-



mienta Barrios 1990). Such fodder could be used in California as an input to the state's livestock and poultry sector, which is responsible for 10% of the state's agricultural revenue (California Department of Food and Agriculture 2001). In any case, the market for cactus fruits, which had been restricted for cactus pears in Mexico and southern Italy as well as for pitahayas in southeastern Asia, has recently expanded globally. The establishment of new plantations of these and other edible cacti in California, for domestic consumption by ethnic groups who traditionally consume cacti plus others who are developing a taste for these exotic fruits plus exportation, could contribute to the diversification of revenue production for this leading agricultural state.

#### ACKNOWLEDGMENTS

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SIX NEW SPECIES AND TAXONOMIC REVISIONS IN MEXICAN  
*GAUDICHAUDIA* (MALPIGHIACEAE)

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ABSTRACT

Six new species in the genus *Gaudichaudia* are described and sectional taxonomy in the genus is revised in accordance with findings from molecular analysis of chloroplast and nuclear genomes. *Gaudichaudia cycloptera*, *G. chasei*, and *G. mcvaughii* are removed from section *Gaudichaudia* and placed in section *Cyclopterys*. *Gaudichaudia krusei* and *G. subverticillata* are removed from section *Gaudichaudia* and placed in section *Archaeopterys*. *Gaudichaudia hirtella*, comb. nov. is placed in section *Oligopterys* to accommodate the finding that *Aspicarpa*, at least in part, is nested within *Gaudichaudia*. Three nothosections are named to accommodate new species described as amphiploids among sections. *Gaudichaudia implexa* is described as a new amphiploid species formed from lineages in section *Tritomopterys* and section *Gaudichaudia* (nothosection *Tritomochaudia*). *Gaudichaudia symplecta* and *Gaudichaudia synoptera* are described as two new amphiploid species formed from lineages in section *Tritomopterys* and section *Cyclopterys* (nothosection *Cyclotomopterys*). *Gaudichaudia zygotera* and *Gaudichaudia intermixteca* are described as two new amphiploid species formed from lineages in section *Tritomopterys* and section *Zygoterys* (nothosection *Zygotomopterys*). *Gaudichaudia andersonii* is described as a new amphiploid species formed from lineages within section *Cycloptera*.

RESUMEN

Se describen seis especies nuevas en el género *Gaudichaudia* y se revisa la taxonomía seccional en el género de acuerdo con los hallazgos del análisis molecular del cloroplasto y de los genomas nucleares. Se quitan *Gaudichaudia cycloptera*, *G. chasei* y *G. mcvaughii* de la sección *Gaudichaudia* y se colocan en la sección *Cyclopterys*. Se quitan *G. krusei* y *G. subverticillata* de la sección *Gaudichaudia* y se colocan en la sección *Archaeopterys*. Se pone *Gaudichaudia hirtella*, comb. nov. en la sección *Oligopterys* para acomodar el hallazgo de que *Aspicarpa* por lo menos en parte, se anida dentro de *Gaudichaudia*. Se nombran tres nothosecciones para acomodar la nuevas especies descrita como anfiploide entre secciones. Se describe *Gaudichaudia implexa* como una nueva especie anfiploide formada de linajes en la sección *Tritomopterys* y la sección *Gaudichaudia* (nothosección *Tritomochaudia*). Se describen *Gaudichaudia symplecta* y *Gaudichaudia synoptera* como dos especies nuevas del anfiploide formada de linajes en la sección *Tritomopterys* y la sección *Cyclopterys* (nothosección *Cyclotomopterys*). Se describen *Gaudichaudia zygotera* y *Gaudichaudia intermixteca* como dos especies nuevas del anfiploide formada de linajes en la sección *Tritomopterys* y la sección *Zygoterys* (nothosección *Zygotomopterys*). Se describe el *Gaudichaudia andersonii* como una especie nueva del anfiploide formado de linajes dentro de la sección *Cycloptera*.

Key Words: Amphiploid, *Gaudichaudia*, polyploid complex, Malpighiaceae, nothospecies, systematics.

*Gaudichaudia* (Malpighiaceae) is a genus of woody vines, vining shrubs, and suffrutescent shrubs inhabiting xeric to mesic habitats in Mesoamerica and northern parts of South America. Most of the diversity in *Gaudichaudia* is geographically concentrated in central, western and southern Mexico with variable wide-ranging lineages reaching into northeastern and northwestern Mexico, and south into Central America and northern South America. Several regional and narrow endemics occur in central Mexico south of the Tropic of Cancer and west of the Isthmus of Tehuantepec. *Gaudichaudia* was monographed by Franz Niedenzu in 1928, but little progress was made in understanding the genus until the work of Anderson in the 1980's. Niedenzu attempted to coordinate the prior works of de Candolle, Adrien de Jussieu, Sessé and Mochoño, Kunth, Chodat, Rose, and others who had de-

scribed taxa in the genus in the previous century. Niedenzu himself added numerous names, constructing an elaborate taxonomic system that included two subgenera and three sections covering eleven species and twenty-three infraspecific taxa. Although Niedenzu proliferated names in the genus, he also significantly reduced the nomenclatural superfluity in *Gaudichaudia* by listing twenty-nine names from five genera in synonymy. While Niedenzu's work was a significant step in clarifying the systematics of *Gaudichaudia*, the profusion of names he introduced had the opposite effect. Niedenzu's taxa were largely based on narrow taxonomic concepts that relied on characters that are now clearly seen as variable within lineages and sometimes plastic even within a single individual. For example, he used the number of glands on the calyx to diagnose forms within varieties within sub-

species in both *G. cycloptera* and *G. cynanchoides*. Furthermore, Niedenzu's reliance on floral features in *Gaudichaudia*, which like other Malpigiaceae is distinctive in the ancient (Taylor and Crepet 1987) and conservative features of its flowers (Anderson 1979), yielded a taxonomy that overlooked some distinctive species while emphasizing relatively minor variations in widespread taxa. To further confound taxonomic matters in *Gaudichaudia*, the herbarium specimens available to Niedenzu for his monograph were largely collected prior to 1910, and most of the collections he cited, even those designated as types, are lacking specific locality data. Some of the types are fragmentary or consist of immature stages, in a few cases without fruits or mature flowers. The names based on inadequate type material may never be clearly referable to a lineage and are therefore of little or no taxonomic value today.

Taxonomy in *Gaudichaudia* has been revisited in recent years by Anderson (1987, 1993), who clarified some of the nomenclature and described three new species that were missed by Niedenzu and his predecessors. Anderson (1993) accepted Niedenzu's sectional taxonomy: section *Tritomopterys*, section *Zygopterys*, and section *Gaudichaudia*, all of which are distinguished on fruit wing morphology. Fruit wing morphology in section *Tritomopterys* (*G. albida* Schlecht. & Cham., *G. diandra* (Nied.) Chodat, *G. hexandra* (Nied.) Chodat) is characterized by highly asymmetric lateral wings (Fig. 1), and in section *Zygopterys* (*G. galeottiana* (Nied.) Chodat) by distally rounded, free and symmetric lateral wings, and a well developed posterior wing (Fig. 2). Section *Gaudichaudia* is characterized by a rounded fruit wing with the apex sometimes notched, but with lateral wings scarcely free at the apex and completely confluent at the base (Fig. 2). Anderson (1993) includes *G. cynanchoides* H. B. K., *G. cycloptera* (DC.) W. R. Anderson, *G. subverticillata* Rose, *G. chasei* W. R. Anderson, *G. mcvaughii* W. R. Anderson, and *G. krusei* W. R. Anderson in section *Gaudichaudia* (Fig. 2 in part, Figs. 3, 4). Anderson's (1987, 1993) published work on *Gaudichaudia* recognizes ten species, including the three he described (*G. mcvaughii*, *G. krusei*, *G. chasei*). Anderson (1993) has shown that all ten of the recognized species are diploids with  $n = 40$  meiotic chromosome pairs. Anderson (personal communication) also recognizes several species in *Gaudichaudia* that have yet to be published. Three of those (species-A, "*G. intermedia*"; species-B, "*G. hirsuta*"; species-C, "*G. velutina*") are clearly in section *Tritomopterys* and closely related to the *G. albida*—*G. diandra*—*G. hexandra* complex (Fig. 1). At least some of the undescribed species in section *Tritomopterys* are also known diploids as shown by Anderson's (1993) chromosome counts published as *G. albida* sens. lat. Another undescribed species in *Gaudichaudia* is a very distinctive close relative of *G. cycloptera* (species-D,

"*G. mexiae*") that is narrowly restricted to lower elevations in remote areas on the west slopes of coastal Jalisco, Nayarit and Sinaloa (Fig. 3). Judging from morphology of the samaras and the limited chromosome counts available, all of these undescribed elements of *Gaudichaudia* would be easily accommodated within the sections established by Niedenzu as endorsed by Anderson. While the sectional taxonomy in *Gaudichaudia* based on fruit wing morphology is supported by overall morphological similarity of the fruits, recent evidence from comparative analyses of the chloroplast and nuclear genomes (Jessup 1994, 2002), clearly shows that section *Gaudichaudia* as previously constructed is not monophyletic. In this paper I briefly summarize molecular evidence supporting sectional revisions in *Gaudichaudia* and propose a new combination resulting from the finding that *Aspicarpa* is, at least in part, nested within *Gaudichaudia* (Cameron et al. 2001; Davis et al. 2001). I propose three new sections and three new nothosections in *Gaudichaudia* and reclassify anomalous species. Six new species are described.

#### MOLECULAR EVIDENCE

Total genomic DNA was extracted from 118 *Gaudichaudia* specimens collected across a wide geographic region of Mexico. Extraction protocol and restriction site analysis followed procedures outlined in Dowling et al. (1996). Accession data and detailed laboratory procedure is presented in Jessup (1994). Restriction sites found on the chloroplast genome are presented in Table 1. Twenty-one informative sites were produced with 10 of the 20 enzymes screened. Thirty-four distinct chloroplast haplotypes were discovered, each present in between 1 and 29 specimens. Restriction site data for representatives of each of the 34 haplotypes is given in Table 2. Phylogenetic analysis of the cpDNA data was performed with Hennig 86 v.1.5 (Farris 1989). Autapomorphies were excluded from the analysis. The procedure "mhennig\*" was used to search for the shortest possible trees. Branch swapping on the shortest trees found by multiple initial passes with different OTU addition sequences produced a set of trees that was then used as the starting point for procedure "bb", an extended branch-swapping algorithm that searches all possible trees. As a check on thoroughness of the heuristic algorithms, a separate run of the procedure "-ie; bb", an implicit enumeration algorithm followed by branch-swapping, was used to find all of the shortest trees, which were then used to compute the majority rule consensus tree using PAUP (Swofford 1990).

The majority rule consensus tree of 26 equally parsimonious trees obtained from restriction site characters is presented in Fig. 5. Terminal branches in the cpDNA tree represent the 34 distinct genomes discovered in the sample of 118 plants. Ro-

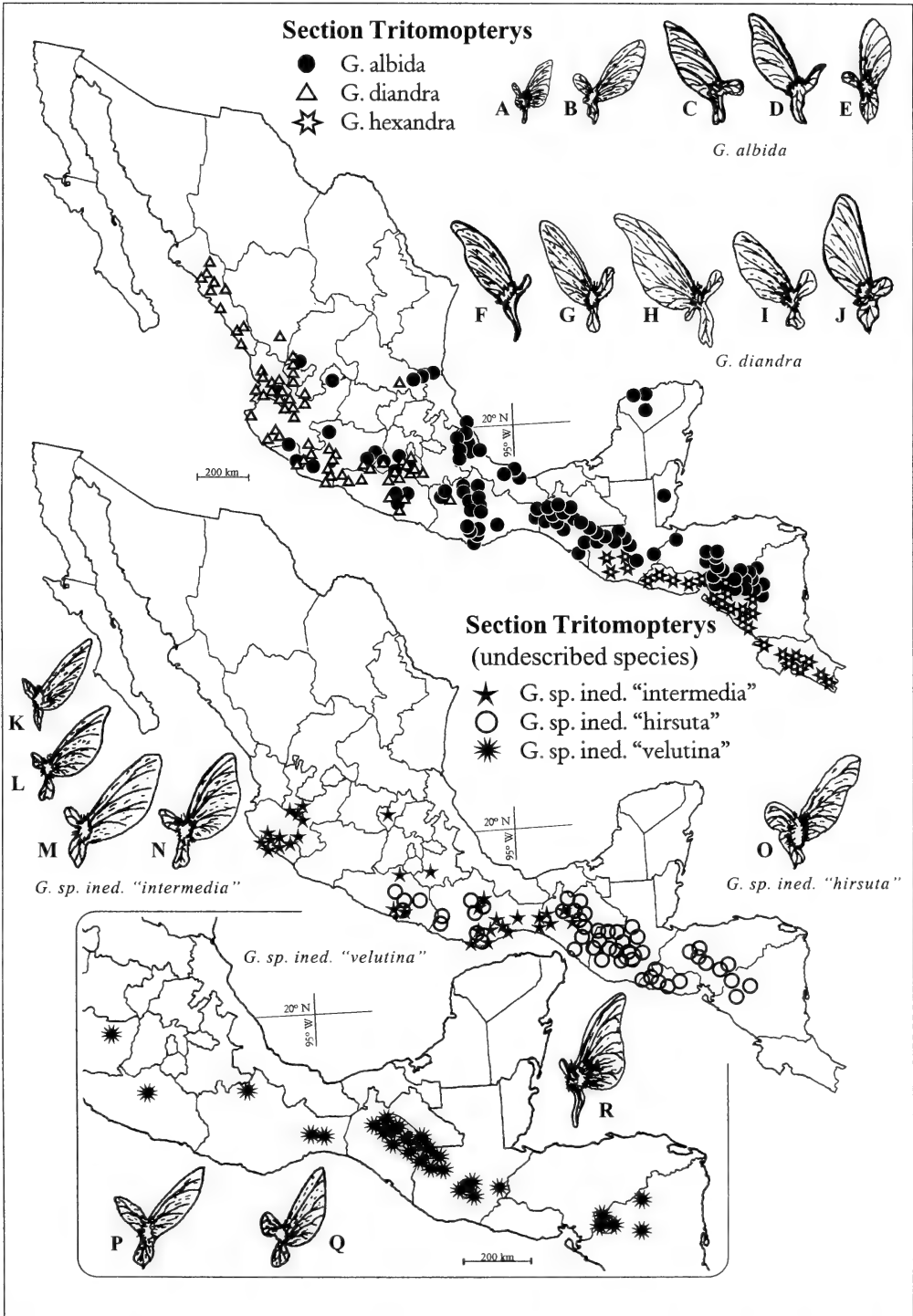


FIG. 1. Geographic distribution of species and fruit morphology in representative collections from section *Tritompterys*. A–E, *G. albida*, A) Jessup 4041, Oaxaca, B) Jessup 4052, C) Anderson 13275, Mexico, D) Jessup 4067, Guerrero, E) Jessup 4056, Chiapas; F–J, *G. diandra*, F) Jessup 4088, Nayarit, G) Jessup 4066, Guerrero, H) Anderson 13309, Michoacan, I) Jessup 4032, Michoacan, J) Anderson 12937, Morelos; K–N, *G. sp. ined. "intermedia"*, K) Anderson 13225, Chiapas, L) Jessup 4051, Oaxaca, M) Anderson 13224, Chiapas, N) Jessup 4055, Chiapas; O, *G. sp. ined. "hirsuta"*, Jessup 4048, Oaxaca; P–R, *G. sp. ined. "velutina"*, P) Jessup 4058, Chiapas, Q) Jessup 4060, Chiapas, R) Jessup 4054, Oaxaca. Samara illustrations are approximately 1×.

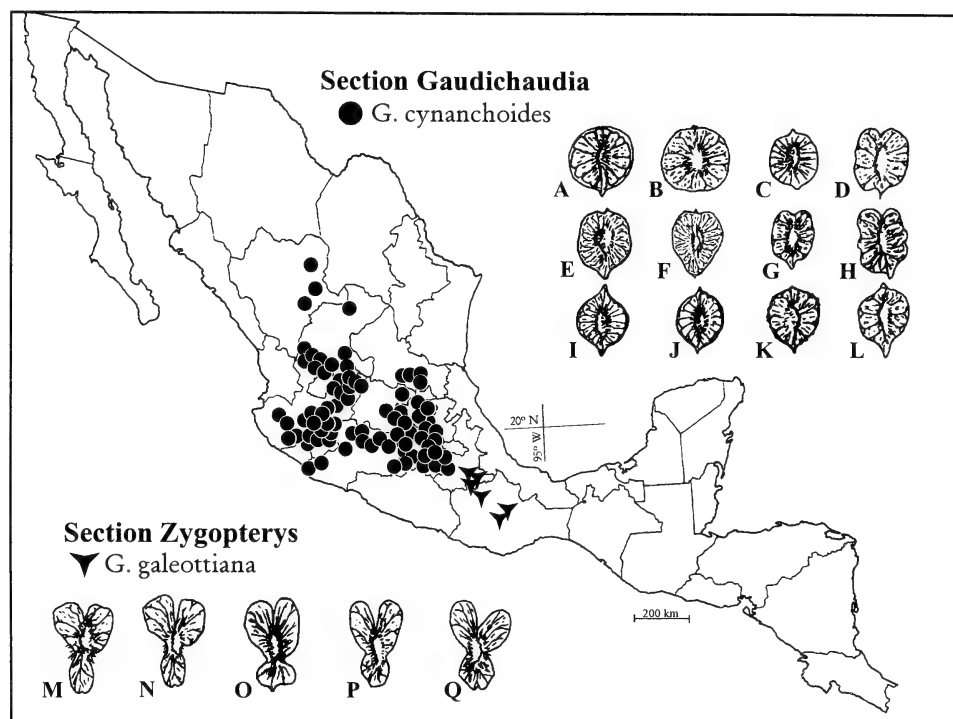


FIG. 2. Geographic distribution of species and fruit morphology in representative collections from section *Gaudichaudia* and section *Zygopterys*. A–L, section *Gaudichaudia*: A) Jessup 4078, Jalisco, B) Koch 82260, Mexico, C) Jessup 4077, Jalisco, D) Nicolas 5078, Puebla, E) Jessup 4075, Michoacan, F) Anderson 13296, Michoacan, G) Jessup 4111, Hidalgo, H) Anderson & Laskowski 3884, Michoacan, I) Jessup 4112, Hidalgo, J) Jessup 4109, Hidalgo, K) McVaugh 13204, Michoacan, L) Anderson & Laskowski, Michoacan; M–Q, section *Zygopterys*: M–N) *Galeotti* X. 1844, Tutepeji, Puebla (type), O) Jessup 4038, Puebla, P) Anderson & Laskowski 4294, Puebla, Q) Anderson 13128, Oaxaca. Samara illustrations are approximately  $1\times$ .

busness of the phylogenetic estimate is indicated by the fact that all but two branches are supported by 100% of the trees in the consensus calculation. Detailed geographic mapping of the cpDNA haplotypes and taxonomic assignment of plants carrying those chloroplast genomes is presented in Jessup (1994). The cpDNA phylogeny taken together with morphological features supports recognition of six sections in *Gaudichaudia*. Sections *Tritompterys* and *Zygopterys* as recognized by Anderson (1993) are well supported as monophyletic by the cpDNA analysis. Section *Gaudichaudia* is monophyletic with the removal of *G. cycloptera*, *G. mcvaughii*, *G. chasei*, *G. subverticillata*, and *G. krusei*. The geographically widespread species *G. cynanchoides* is shown to be a genetically diverse assemblage of morphologically similar lineages. The methods used in this study were unable to resolve the basal polytomy. The cpDNA phylogeny is illustrated as an unbranched network (Fig. 5) to emphasize the lack of phylogenetic resolution among the sections in *Gaudichaudia*.

To accommodate the species removed from section *Gaudichaudia* two new sections are proposed here; section *Cyclopterys* and section *Archaeopter-*

*ys*. Section *Cyclopterys* is well supported by the cpDNA analysis as monophyletic and includes *G. cycloptera*, *G. mcvaughii*, and *G. chasei*, as well as the undescribed elements discussed above. Section *Archaeopterys* is paraphyletic and, based on morphological evidence and evidence from analysis of nuclear DNA discussed below, comprises a cluster of phylogenetically basal lineages within the genus. There is not, however, sufficient evidence to root the cpDNA network with section *Archaeopterys*. Section *Oligopterys* is proposed here to accommodate species of *Aspicarpa* that have been found to nest within *Gaudichaudia*, as reported by Cameron et al. (2001), Davis et al. (2001) and Jessup (1994).

#### TAXONOMIC REVISIONS AND NEW SPECIES

##### *Revision of sectional taxonomy of the diploid species.*

**Sectio *Cyclopterys*** Jessup sect. nov. (Fig. 3)—  
TYPE: Mexico, Michoacan: Tuzantla, 110 km N Huetamo, rd to Zitacuaro, 670 m. 15 October 1988, Jessup 4033 (Holotype MICH; isotypes MO, UC, IEB).

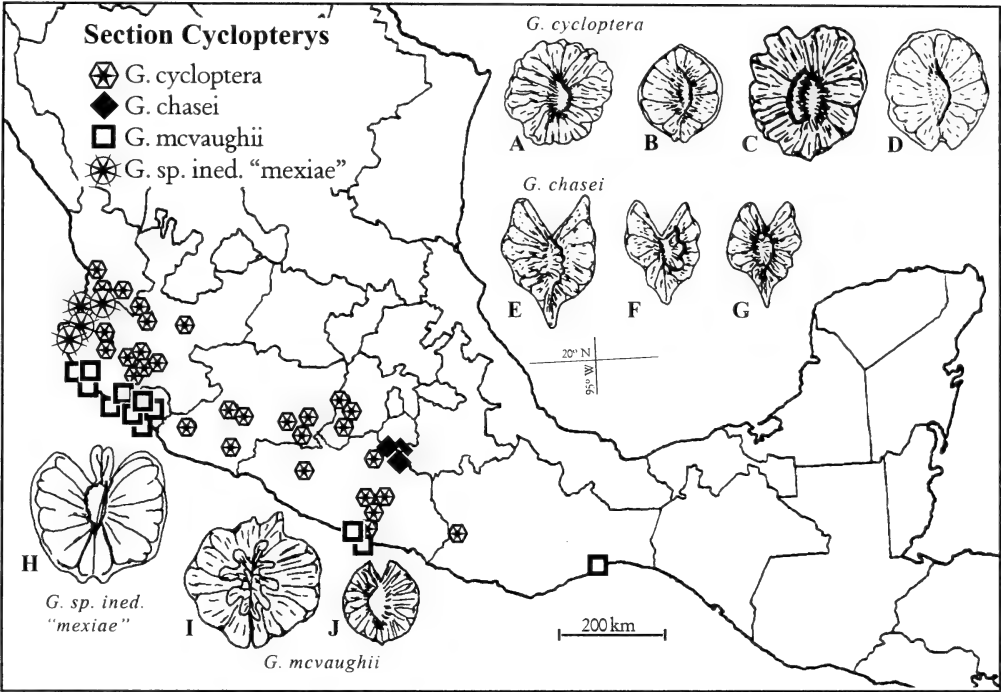


FIG. 3. Geographic distribution of species and fruit morphology in representative collections from section *Cyclopterys*. A–D, *G. cycloptera*, A) Jessup 4029, Guerrero, B) Jessup 4083, Jalisco, C) Jessup 4033, Michoacan, D) McVaugh & Koelz 534, Nayarit; E–G, *G. chasei*, E) Lyonnet 28, Morelos, F) Jessup 4009, Morelos, G) Bates 3426, Morelos; H) *G. sp. ined. "mexiae"*, Croat 45249, Nayarit; I–J, *G. mcvaughii*, I) Anderson 12699, Colima, J) Koch & Fryxell 82218, Guerrero. Samara illustrations are approximately 1×.

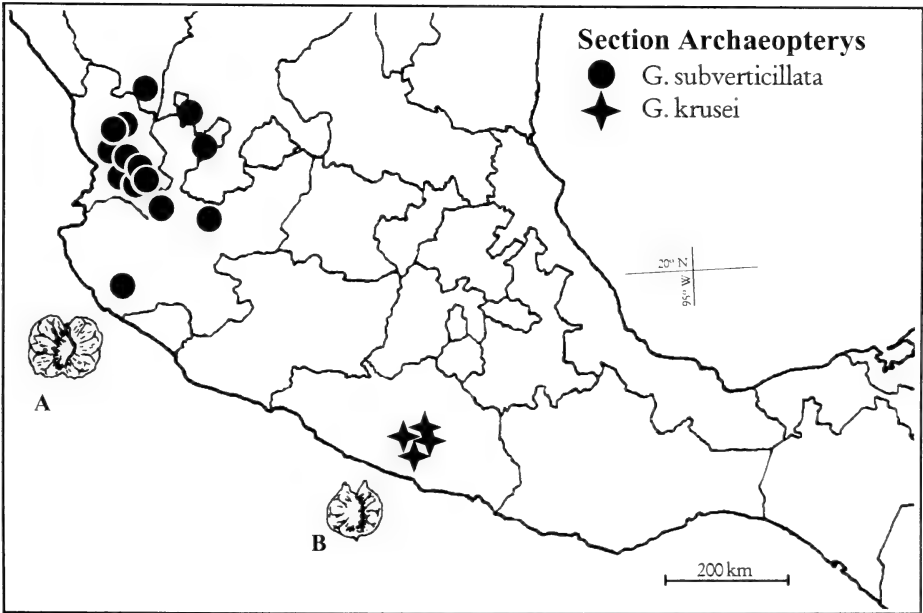


FIG. 4. Geographic distribution of species and fruit morphology in representative collections from section *Archaeopterys*. A) *G. subverticillata*, Jessup 4087; B) *G. krusei*, Jessup 4069. Samara illustrations are approximately 1×.

TABLE 1. INFORMATIVE cpDNA RESTRICTON SITES FOUND IN 118 SPECIMENS. Each restriction site is represented by a letter code and referred to in the data matrix in Table 2.

Enzyme	Informative site(s)	Site code
Ban II	9.6 → 8.2 + 1.4	Q
Bcl I	4.4 → ? + ?	H
	3.6 → 2.1 + 1.5	O
	3.5 → 2.0 + 1.5	T
Cla I	19.0 → 8.2 + 10.8	E
	2.8 → 1.2 + 1.6	F
	2.9 → 1.3 + 1.6	G
Dra I	6.15 → 5.48 + .67	K
	5.48 → 4.2 + 1.28	L
	3.1 → 1.6 + 1.5	M
Eco RI	3.5 → 3.0 + 0.5	A
Eco RV	16.5 → 9.5 + 7.0	D
Hae III	4.8 → 1.3 + ?	I
	1.4 → 1.2 + 0.2	J
	1.6 → ? + ?	R
	2.3 → ? + ?	S
Hinc II	5.6 → 3.5 + 2.1	P
	4.3 → 2.3 + 2.0	U
Hpa II	5.1 → 3.6 + 1.5	N
Xba	3.8 → 2.0 + 1.8	B
	3.8 → 2.5 + 1.3	C

To promote nomenclatural clarity, and to bring evidence from DNA analyses to bear on taxonomic circumscription of this section, under provisions of the ICBN Saint Louis Code, Article 22.6 (Greuter et al. 2000), I am designating a different holotype for section *Cyclopterys* than the type for the name on which the section is based, which is *Gaudichaudia cycloptera* (DC.) Anderson. The earliest name for the species according to Anderson (1987) is *Hiraea? cycloptera* DC. Prodr. 1: 586. 1824, and the type for that name is an unnumbered illustration among de Candolle's collection of plates, referred to simply as "fl. mex. ic. ined." (de Candolle 1824), a plate presumably copied from Sessé and Mociño's original painting in the *Icones Florae Mexicanae*, now at HU. The original watercolor illustration, the presumed virtual type, was titled, "*Triopteris oblongifolia*" (HU accession number 6331.0888). Many of the 279 names based on types that are plates or copies of plates from the Sessé and Mociño expedition were never vouchered with a collection (McVaugh 1980). This is most likely the case for *G. cycloptera*. So far as I am aware there is no known specimen corresponding to the plate, though the possibility remains that a specimen will be found in MA or among the collections belonging to a recipient of specimens collected on the Sessé and Mociño expedition. Establishment of section *Cyclopterys* is warranted on the evidence from DNA analyses together with morphological comparisons. I am designating a type for the section that can be subjected to further DNA analysis. The specimen designated as holotype for the section carries cpDNA haplotype Z, one of five haplotypes found in a well supported monophyletic *G.*

*cycloptera* (Fig. 5). *G. cycloptera* bearing cpDNA haplotype Z has not been discovered as a component in any amphiploid formed among sections in *Gaudichaudia*, although the closely related cpDNA haplotype AB is shared between some lineages within section *Cyclopterys*, in particular between *G. cycloptera* and *G. mcvaughii*, (Jessup 1994).

Herbae frutescens scandentes e basi fruticosa, caulibus longissimis volubilibus in vegetationem sustentem extendentibus 4–12 m. Folia decussata et sensim decrescentia a basi ad ramos distales florescentes, late elliptica ad ovata, subsessilia ad distincte petiolata, basi hastata, cordata, truncata, vel cuneata. Indumentum partes maturas vegetativas totae plantae tegens, dense sericeum vel sparse hirsutum ad grosse hispidum, e trichomatibus ramosis constans, trabeculis laevibus ad sinuosis, adpressis ad erecto-patentibus vel subaristatis. Flores omnes chasmogami, ad anthesin 1.5–3 cm lati, in umbellis geminatis 4-floris in axillis foliorum reductorum vel in dichasiis foliosis axillaribus dispositi, interdum in thyrsus elongatum distaliter fasciculati. Samarae orbiculares ad cordatae, 1–2 cm in diametro, alis lateralibus symmetricis, ad carpophorum confluentibus et rotundatis ad acutis vel late retusis, lobis apicalibus alarum obtusis ad acutis incisuram sinu lato ad angusto facientibus, vel alis lateralibus confluentibus ad apicem, margine distali itaque integra. Superficies dorsalis fructus alam distinctam interdum prominentem vel reticulum congestum penularum supra nucem ferens.

Vines and vining shrubs from a shrubby base, the longest twining stems reaching 4–12 m into the supporting vegetation. Leaves decussate and gradually reduced from the base to the distal flowering branches, broadly elliptic to ovate, subsessile to distinctly petiolate, leaf bases hastate, cordate, truncate or cuneate. Vesture thinly or densely sericeous or sparsely hirsute to coarsely hispid, comprising branched trichomes, the trabeculae smooth to sinuose and appressed to erect spreading or subaristate, the indumentum covering mature vegetative parts of entire plant. Flowers all chasmogamous, 1.5–3 cm in diameter at anthesis, on paired four-flowered umbels in the axils of reduced leaves, or in axillary leafy dichasia, sometimes clustered distally to form an elongate thyrsus. Samaras orbicular to cordate, 1–2 cm in diameter, the lateral wings symmetric, confluent and rounded to acute or broadly retuse at the carpophore, the apical wing lobes obtuse to acute, forming a notch with a broad to narrow sinus, or the lateral wings apically confluent, the distal margin thus entire. The dorsal surface of the fruit bearing a distinct, sometimes prominent wing or a congested nexus of winglets over the nut.

Phylogenetic analysis of restriction sites in the chloroplast genome of *Gaudichaudia* (Fig. 5) clearly supports Niedenzu's section *Tritomopterys* containing lineages related to *G. albida*. The phylogenetic analysis also supports section *Gaudichau-*



TABLE 2. cpDNA RESTRICTION SITE MATRIX FOR HAPLOTYPES. Restriction site codes refer to Table 1. Each haplotype is designated by 1–2 letters.

Haplotype	Specimen	Estado	Sites (refer to Table 1)
			ABCDEFGHIJKLMNQRSTU
A	J4047	Oaxaca	000101000000110000000
B	J4059	Chiapas	000111000000110000001
C	J4055	Chiapas	010111000000110000001
D	J4015	Morelos	000111000100110000001
E	J4036	Michoacan	000111000100100000000
F	J4056	Chiapas	000110000100110000001
G	J4103	Zacatecas	00011100000001010010
H	J4064	Guerrero	001111000000100000000
I	J4087	Nayarit	101111000000100000000
J	J4069	Guerrero	011111000000100000000
K	A13216	Oaxaca	010111101000110100000
L	J4027	Guanajuato	000111101000110100000
M	A3707	Jalisco	000111101000010100000
N	J4102	Sinaloa	000110101000110100000
O	J4008	Morelos	000111101000110000000
P	J4035	Michoacan	100111000000101011011
Q	J4037	Michoacan	101111000000101011011
S	J4081	Jalisco	101111000000001011010
T	J4018	Morelos	101111000000001011010
R	J4007	Guanajuato	101111000000001011010
U	J4112	Hidalgo	101111000000001011010
V	J4042	Oaxaca	0011110100101000000100
W	J4049	Oaxaca	1011110100101000000100
X	A12990	Oaxaca	1011110000101000000100
Y	J4029	Guerrero	101001000000100000000
Z	J4033	Michoacan	101001000000100000000
AA	J4030	Michoacan	001001000000100000000
AB	J4024	Mexico	101011000000100000000
AC	A12699	Colima	101010000000100000000
AD	J4038	Puebla	1011110000011000000101
AE	J4009	Morelos	101111000000100000000
AF	A4510	Guerrero	101111000000000000000
AG	J4039	Puebla	0011110000011000000101
Putative outgroup		Apsicarpa	101111000000100000000

dia containing lineages related to *G. cynanchoides*, as well as section *Zygopterys* containing the single species, *G. galeottiana*. In the phylogenetic analysis section *Zygopterys* and section *Tritompterys* were each found to be monophyletic. Based on the molecular data, however, a monophyletic section *Gaudichaudia* cannot include *G. cycloptera*, *G. mcvaughii*, *G. subverticillata*, *G. krusei*, or *G. chasei* as proposed by Anderson (1993). Those species are therefore moved to new sections as detailed below. Section *Cyclopterys* is strongly supported as monophyletic by the chloroplast DNA phylogeny, comprising the distinctive and geographically widespread type species, *G. cycloptera* and the narrow endemic, *G. mcvaughii*, known only from scattered and narrowly delimited low elevation localities on the Pacific coast of Colima, Guerrero, and Oaxaca. In addition to sharing, in some populations, a distinct chloroplast haplotype with *G. cycloptera*, *G. mcvaughii* also shares morphological features of the fruit and habitat attributes with *G. cycloptera*. The

elaboration of a dorsal wing in the fruits of both species, and the size and shape of the fruits provide further evidence that these taxa are closely related. Both *G. cycloptera* and *G. mcvaughii* are plants of mesic understory or forest edge thickets. Both are known diploids without cleistogamous flowers. Although the branch supporting the single collection of *G. chasei* included in the analysis (Fig. 5) is unresolved with respect to branches supporting sections, *G. chasei* has several morphological features in common with members of section *Cyclopterys*, notably the expanded dorsal keel on the samara, and lateral fruit wings that are basally confluent. *Gaudichaudia chasei*, which Anderson (1987) argues is morphologically close to *G. mcvaughii*, is known from only a small area in Morelos. The habitat where it grows is more similar to the mesic understory habitat of *G. cycloptera* from adjacent Edo. Mexico than the habitat of the typical species of section *Gaudichaudia* (*G. cynanchoides*), which grows in the xeric matorral of the Al-

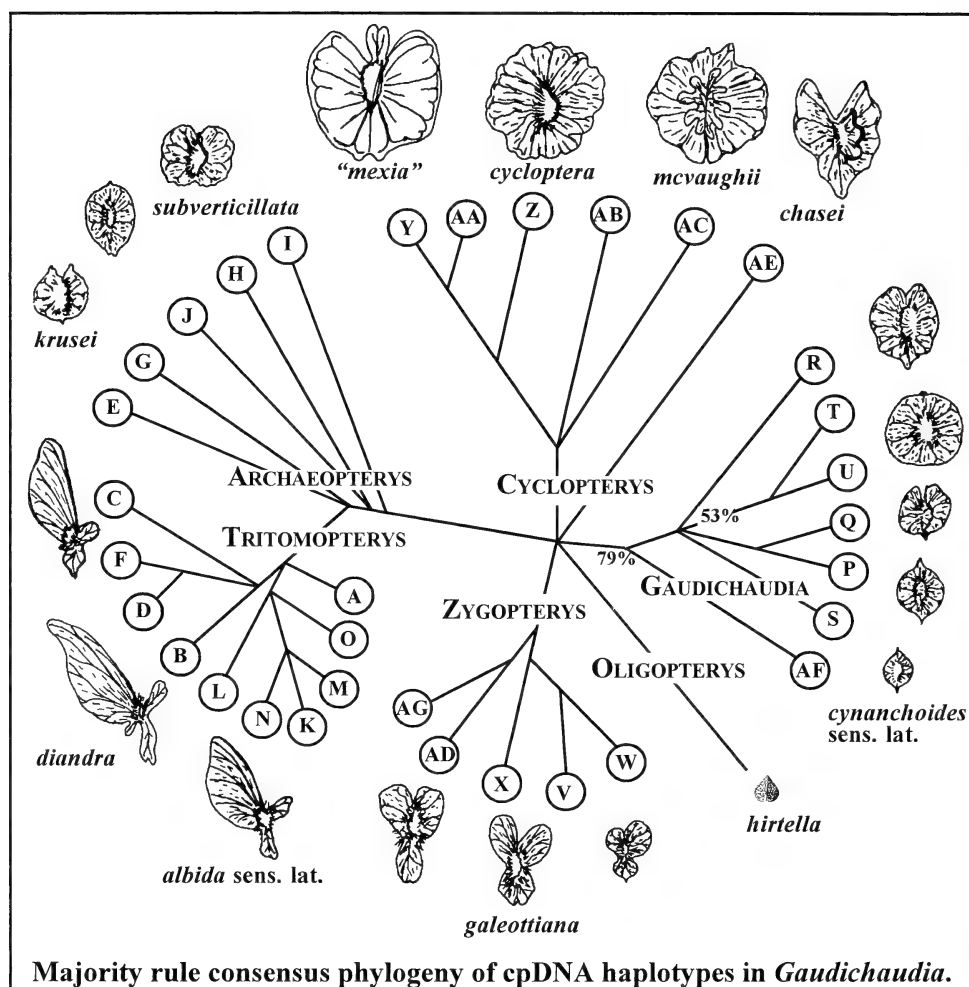


FIG. 5. Majority rule consensus phylogeny of cpDNA haplotypes showing the relationship of sections in an unrooted network. Each terminal branch represents a distinct cpDNA haplotype defined by a unique configuration of restriction sites. Letters in circles designate haplotypes referred to in Table 2. Representative fruits of species of non-hybrid origin illustrate the range of fruit morphology in each section. Position of the fruits relative to branches of the network is approximate.

toplano Mexicano (Fig. 2). *Gaudichaudia chasei*, like *G. cycloptera* and *G. mcvaughii*, lacks the cleistogamous flowers that are a prevalent feature in *G. cynanchoides*. Though perhaps a divergent member of section *Cyclopterys*, *G. chasei* clearly fits better here than in the other sections and is not otherwise sufficiently distinct to justify a separate section. The molecular evidence, absence of cleistogamy and other morphological evidence mentioned by Anderson (1987), the similarity of geographic range and habitats, and the evidence from Anderson's (1993) study of chromosomes, indicating that all are diploids with  $n = 40$  meiotic chromosome pairs, taken together strongly supports recognition of section *Cyclopterys*, containing *G. cycloptera*, *G. mcvaughii*, *G. chasei*, and the undescribed lineage

from Nayarit and Jalisco (*G. sp. ined. "mexiae"*) as a discernable monophyletic clade within *Gaudichaudia*.

Section *Gaudichaudia* sensu Anderson (1993) included *G. subverticillata* and *G. krusei*, two species that he argued are closely related (Fig. 4). Both are subshrubs with rounded fruit wings resembling in outline the fruits of *G. cynanchoides*. The phylogeny based on chloroplast genomes does not, however, support inclusion of those species in a monophyletic section *Gaudichaudia*. The fruits are generally similar in size and shape to those of section *Gaudichaudia*, and are quite distinct from fruits of species included in section *Tritompterys*. Nevertheless, *G. subverticillata* and *G. krusei* are unambiguously placed as outgroups to the *G. al-*

*bida* complex (section *Tritomopterys*) in the parsimony analysis of the chloroplast genomes (Fig. 5). Taken together, *G. subverticillata*, *G. krusei* and section *Tritomopterys* are monophyletic. In view of the substantial divergence in gross morphology between *G. subverticillata* and *G. krusei* on the one hand and members of section *Tritomopterys* on the other, however, their assignment to section *Tritomopterys* is untenable. *Gaudichaudia subverticillata* and *G. krusei* are certainly similar in morphology: both are suffrutescent shrublets lacking cleistogamy, and both are known diploids. They occupy similar habitats, and are both narrow endemics in a region of southwestern Mexico rich in narrow endemics from many groups of plants, a fact that suggests the area may have served as an ancient refugium where phylogenetically basal lineages might be expected to persist. Furthermore, the comparative analysis of nuclear genomes based on randomly amplified DNA (Jessup 2002) places *G. subverticillata* and *G. krusei* as sister taxa close to members of section *Cyclopterys*, but on the periphery of the minimum spanning tree of Jaccard distances. The evidence, taken together, corroborates the hypothesis that *G. subverticillata* and *G. krusei* are basal within *Gaudichaudia*. They are apparently closely related to each other, and more closely related to section *Tritomopterys* and section *Cyclopterys* than they are to section *Gaudichaudia*. To accommodate sectional placement of *G. subverticillata* and *G. krusei* the following new section is established.

Seccio **Archaeopterys** S. L. Jessup sect. nov.

Fruticuli suffrutescentes raro ramosi, ramis maximis plerumque 0.5–1.0 m altis e basi lignosa. Folia brevipetiolata ad subsessilia, binata vel verticillata terna. Indumentum partes maturas vegetativas totae plantae tegens, sparse vel dense sericeum ad velutinum, e trichomatibus ramosis constans, trabeculis laevibus ad sinuosis et adpressis ad erecto-patentibus. Flores omnes chasmogami, in umbellis 4-floris verticillatis e nodis distalibus caulium primorum vel in dichasiis brevibus axillaribus a foliis caulinis superioribus subtentis dispositi. Samarae orbiculares ad cordatae, alis lateralibus symmetricis, proximaliter acutis vel ad carpophorum infirme retusis, lobis distalibus alarum obtusis ad acutis, incisura apicali sinum obtusum ad acutum facienti, superficies dorsalis fructus alam rudimentariam ad prominentem vel reticulum humile pennularum supra nucem ferens.

Suffrutescent seldom branching shrublets, the largest branches mostly 0.5–1.0 meter high from a woody base. Leaves short petiolate to subsessile, paired or in whorls of three. Vesture thinly or densely sericeous to coarsely velutinous, comprising branched trichomes, the trabeculae smooth to sinuose and appressed to erect spreading covering mature vegetative parts of entire plant. Flowers all

chasmogamous, in verticillate four-flowered umbels from distal nodes of main stems, or on short axillary dichasia subtended by the upper stem leaves. Samaras orbicular to cordate, the lateral wings symmetric, proximally acute to weakly retuse at the carpophore, the distal wing lobes obtuse to acute, the apical notch forming an obtuse to acute sinus, the dorsal surface of the fruit bearing a rudimentary to prominent wing or low nexus of winglets over the nut.

Type: *Gaudichaudia subverticillata* Rose

The problem of long branch attraction makes interpretation of branching order among sections in *Gaudichaudia* problematic. Basal lineages with few close relatives in a genus of otherwise closely related species complexes are particularly sensitive to inaccurate placement. Placement of section *Archaeopterys* should therefore be tempered with skepticism until Tribe Gaudichaudieae can be analyzed as a whole with sequence data chosen specifically for this problem.

With the foregoing sectional reassignments, section *Gaudichaudia* now comprises only vines with both chasmogamous and cleistogamous flowers producing rounded, essentially symmetric (cynanchoid) samaras. Section *Gaudichaudia* as revised includes only *G. cynanchoides* sens. lat., which is widespread in mesic to xeric ruderal habitats on the Altoplano Mexicano (Fig. 2). Although the only accepted species remaining in section *Gaudichaudia* is *G. cynanchoides*, that name as now used encompasses a diverse assemblage of microspecies propagating largely through abundant production of cleistogamous fruits. As evident in the series of distinct chloroplast haplotypes and diverse morphotypes (Jessup 1994), *G. cynanchoides* is a species complex that should eventually be resolved into several closely related but geographically distinct species or subspecies.

In addition to supporting the realignment of sectional taxonomy of recognized members of *Gaudichaudia*, the results of molecular research clearly indicate that the genus *Gaudichaudia* itself, as conventionally delimited, is paraphyletic. My molecular studies (Jessup 1994, 2002) included the genus *Aspicarpa* as the outgroup in several analyses, but in the maximum likelihood analysis (unpublished results) *Aspicarpa* was found to nest within *Gaudichaudia* in a polytomy with section *Cyclopterys*, section *Archaeopterys*, and section *Gaudichaudia*. That result is corroborated by recent molecular phylogenies of the Malpighiaceae (Cameron et al. 2001; Davis et al. 2001) showing that at least some species now included within *Aspicarpa* are nested within *Gaudichaudia*. To accommodate the evidence demonstrating that *Aspicarpa* is, at least in part, nested within *Gaudichaudia*, I here establish a new section in *Gaudichaudia* to include those elements of *Aspicarpa* that are properly considered

species within a monophyletic *Gaudichaudia*. The type of the new section is established by the following new combination.

***Gaudichaudia hirtella* (Rich.) Jessup, comb. nov.**

*Aspicarpa hirtella* Rich., Mem. Mus. Paris 2: 399. 1815.

*Aspicarpa urens* Lagasca, Gen. Sp. Pl. Nov. 1. 1816.

*Aspicarpa pruriens* Desv., Desf. Cat. Hort. Paris. Ed. 3. 233. 1829.

*Gaudichaudia urens* Chodat in Bull. Soc. Bot. Genève 2. Sér. IX. 1917.

**Section *Oligopterys* Jessup sect. nov.**

Fruticuli suffrutescentes caulibus paucis ad multis erectis vel decumbentibus e basi lignosa. Folia opposita vel verticillata, basi rotundata ad cordata, sessilia ad subsessilia. Flores et chasmogami et cleistogami. Fructus sine ala laterali, nuculum oblique affixum sine carpophoro producentes, crista vel jugo dorsali instructi, sine ala dorsali.

Type: *Gaudichaudia hirtella* (Rich.) Jessup, comb. nov.

Suffrutescent shrublets with few to many erect to decumbent or trailing stems from a woody base. Leaves opposite or whorled, rounded to cordate at base, sessile to subsessile. Flowers both chasmogamous and cleistogamous. Fruits lacking a lateral wing, forming an obliquely attached nutlet lacking a carpophore, with a low dorsal crest or ridge, without a dorsal wing.

Other species now placed in *Aspicarpa* will likely emerge as elements of *Gaudichaudia*. Only *G. hirtella* is included here in section *Oligopterys* since that was the species included in my study of chloroplast DNA phylogeny in *Gaudichaudia*. Although the chloroplast DNA parsimony analysis majority rule consensus tree does not resolve the branch supporting *Aspicarpa* with respect to branches supporting other sections, *Aspicarpa* is distinct enough in fruit morphology and plant habit to warrant a separate section. Circumstantial evidence from studies with labeled RAPD probes (Jessup 2002) support placement of section *Oligopterys* close to section *Zygopterys*. When amplified PCR products from *G. galeottiana* were probed against blots of RAPD gels in that study, lanes representing *Aspicarpa* hybridized the probe along with members of section *Zygopterys* and the intersectional amphiploids involving section *Zygopterys*. The probe also weakly hybridized the lane representing *G. krusei*, but did not hybridize lanes representing other lineages within *Gaudichaudia*. In the phenetic analysis of randomly amplified DNA (Jessup 1994) *Aspicarpa* clustered with members of section *Tritomopterys* on the minimum spanning tree of Jaccard distances. Recent DNA sequence analysis of generic phylogeny in Malpighiaceae (Cameron et

al. 2001; Davis et al. 2001) found *Aspicarpa* nested with members of section *Tritomopterys*. Definitive resolution of the phylogenetic placement of sections in *Gaudichaudia* must, however, be deferred until DNA sequences for a broader sample of representative taxa in tribe Gaudichaudieae are available.

*Taxonomic revisions in the amphiploid complexes.* Anderson began the task of resolving reticulate ancestry in *Gaudichaudia*. In addition to his descriptions of new species and chromosome counts in *Gaudichaudia*, Anderson explored the relationship of *Gaudichaudia* to other genera in Tribe Gaudichaudieae (Anderson 1985) and contributed to an understanding of the genus through studies of reproductive life history traits (Anderson 1980). In particular, cryptic self fertilization, which occurs in distinctive cleistogamous flowers, is common to all lineages examined so far that have  $n = 80$  meiotic chromosome pairs. All of the plants examined thus far that bear fruits with morphologies intermediate between those of plants fitting neatly into the sections of *Gaudichaudia* (as herein defined) are tetraploids, and they all bear cleistogamous flowers. The evidence presented by Anderson strongly supports his hypothesis that plants bearing fruits with intermediate morphologies are amphiploids or the products of amphiploids formed among lineages in different sections of *Gaudichaudia*. Results supporting that hypothesis have been corroborated by the results of molecular studies (Jessup 1994, 2002).

The amphiploids present a bewildering mélange of morphological variation that has heretofore been reticent to clean cut species delimitations. The combination of evidence now available from molecular studies and a morphological survey of a large number of collections from across the geographic distribution of *Gaudichaudia* in Mexico, however, reveals several discrete elements among the tetraploids that can be clearly discerned and described as new species in *Gaudichaudia*. Five of the species described here are amphiploids formed among lineages from different sections, and one is apparently formed as an amphiploid among lineages within a section. In each case, the amphiploid origin of the new species is supported by evidence from molecular studies. These are not simple  $F_1$  hybrids, but rather wide-ranging lineages that propagate via selfing through cryptic self fertilization while maintaining outcrossing through chasmogamous flowers. Floral morphology is remarkably uniform across the Tribe Gaudichaudieae, and clearly fits the family-specific floral syndrome associated with oil bee pollination (Buchmann 1987; Vogel 1990). Undescribed diploid lineages identified by Anderson (Figs. 1, 3) are introduced and discussed in this paper in connection with their roles in formation of amphiploids among lineages in different sections of *Gaudichaudia*, and in delimiting new taxa with which they might be confused.

Only amphiploid lineages with unambiguous morphological attributes and clear support from the molecular research are described in this paper. Several additional amphiploid species not treated here remain undescribed in *Gaudichaudia*.

*Nothosections and new amphiploid species.* Provisions are made in the ICBN (Greuter et al. 2000) for naming nothotaxa, taxa of known hybrid origin, and those provisions are codified in the St. Louis Code, Appendix I. A diagnosis or description is not required for the naming of notho-subdivisions of genera, and such names do not have types, but the ICBN requires that names of the parental taxa are specified when the name of the nothotaxon is published (Article H.9). However, species that are known or suspected to be of hybrid origin need not be designated as nothospecies and may be designated as species (Article H.3). Nothosections are proposed here to contain *Gaudichaudia* lineages that are clearly the products of intersectional hybridization. The combined evidence from morphology, chromosomal counts and molecular studies supports designation of nothosections with unambiguous specification of the sectional source of parental lines, even to the point of specifying sectional contributions of the pollen and ovules for individual members of species within the nothosections. Sectional sources of pollen and ovule parents are indicated below for the types and paratypes where known. It has not, however, yet been feasible to unambiguously identify species-level lineages contributing to formation of the species in the nothosections. The species named below can be clearly circumscribed and assigned to nothosections, but which of several possible combinations of species within the parental sections gave rise to them remains unknown or ambiguous. In some cases the member species in nothosections proposed here are likely the products of complex interbreeding among several independently evolving lineages from each of the contributing parental sections. With those reasons in mind the species proposed here are named as species rather than nothospecies.

**Nothosection *Tritomochaudia*** S. L. Jessup nothosect. nov. (*Gaudichaudia* sect. *Gaudichaudia* × *Gaudichaudia* sect. *Tritomopterys*), Fig. 6. Presently I am recognizing only a single broadly delimited species. The molecular data, the chromosome data, and the geographic distribution of morphological variation suggest that this taxon comprises a swarm of autogamously propagating amphiploid microspecies that retain viable chasmogamy.

***Gaudichaudia implexa*** S. L. Jessup, sp. nov. (Fig. 6)—TYPE: Mexico. Jalisco: south shore of Lago de Chapala, 6.4 km W of Jalisco/Michoacan state line, 1620 m, dry thorn scrub in hills above lake, 3 Nov 1988, *Jessup 4076* (Holotype MICH; isotypes CHAP, IEB, UC).

Haec stirps variabilissima a *Gaudichaudia cynanchoides* secedit ala samarae lobos laterales anticos fere symmetricos ad valde asymmetricos acutos ad obtusos rotundatosve formanti, lobis sinu ad basin acuto ad obtuse angulato separatis, sinu interdum denticulo e margine antica alae lateralis vel in basin sinus ex apice nucis orienti, denticulo raro in lobum apicalem rotundatum inter lobos laterales alae crescenti. Samara autem *Gaudichaudia cynanchoides* ala laterali margine apicali fere integra gaudet, et quamquam ala incisuram apicalem parvam exhibet, samara ejus cynanchoidea est et lobis discretis lateralibus sinu profundo separatis numquam instruit. *Gaudichaudia albida*, *Gaudichaudia diandra* et stirpes affines sectionis *Tritomopterygos* statim distinguendae sunt lobis lateralibus alae samarae valde asymmetricis, et cauda angusta postica alae samarae vix vel haud confluenti cum ala laterali. Haec species interdum valde simulabit *Gaudichaudia galeottiana* vel *Gaudichaudia zygoptera* aut alis lateralibus symmetricis rectis aut lobo lato postico constricto ad nucem aut utroque, sed clare distinguenda est limbo texturae inter alas laterales alae posticam et alis lateralibus apicibus obtuse acutis pro alis plerumque latioribus rotundioribusque *Gaudichaudia galeottiana* et *Gaudichaudia zygoptera*; ubicumque autem admiscet speciebus illis, hae differentiae vix discernendae erit. Chromosomatum numerus,  $n = 80$ .

This highly variable species is separable from *G. cynanchoides* by the samara wing forming two approximately symmetric to strongly asymmetric acute to obtuse or rounded anterior lateral lobes apically separated by a sinus that varies from acute to obtusely angular at the base, the sinus sometimes with a small tooth originating from the antical margin of the lateral wing or in the base of the sinus from the crown of the nut, the tooth rarely developing as a rounded apical lobe between the lateral lobes of the wing. By contrast the samara in *G. cynanchoides* has the apical margin of the lateral wing largely entire, and though it occasionally has a small apical notch in the samara wing, the samara is cynanchoid and never has discrete lateral lobes separated by a deep sinus. *Gaudichaudia albida*, *G. diandra* and related species in section *Tritomopterys* can be immediately distinguished by the strongly asymmetric lateral lobes of the samara wing, and by the narrow posterior tail of the samara wing that is scarcely or not at all confluent with the lateral wing. In some cases this species closely resembles *G. galeottiana* or *G. zygoptera* in the development of symmetric upright lateral samara wings or a broad postical lobe constricted where it attaches to the nut. A few specimens bear both of those characteristics, but it is clearly distinguished by a flange of tissue between the lateral wings and the postical wing, and by the lateral wings with bluntly pointed apices rather than the generally broader more rounded wings of *G. galeottiana* and *G. zygoptera*. However, where it hybridizes with those species the

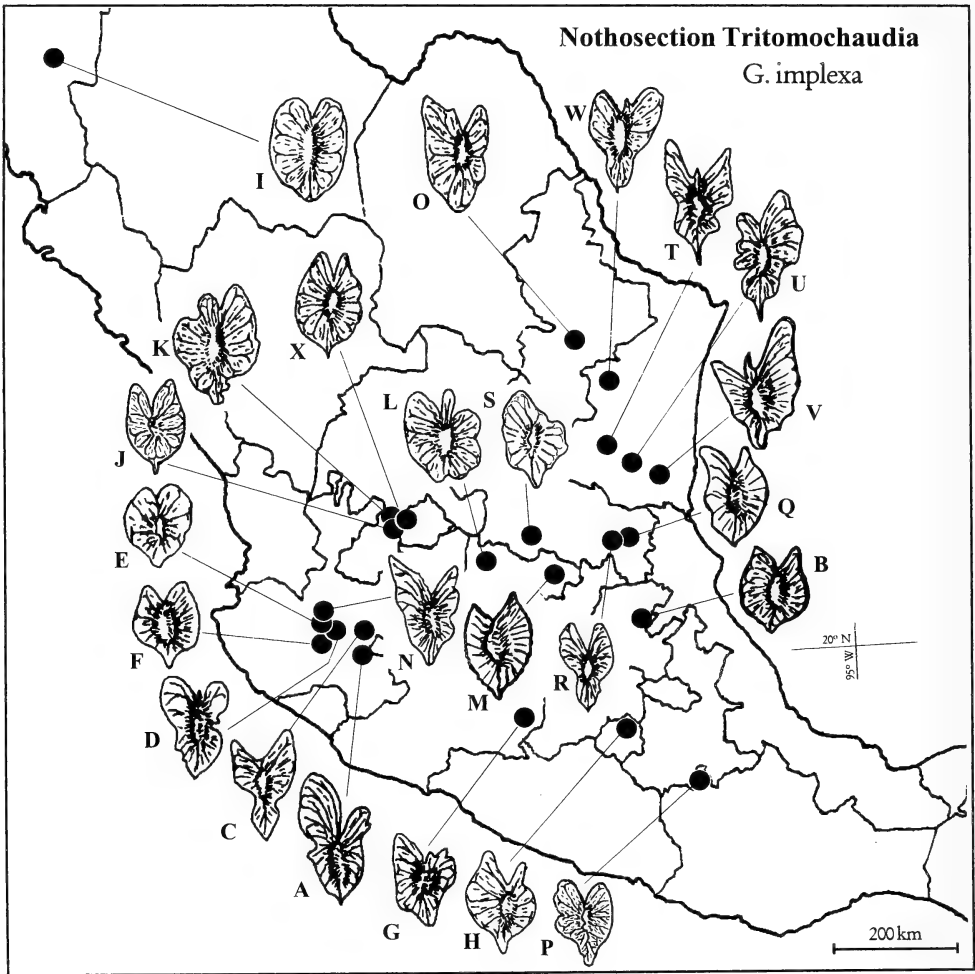


FIG. 6. *Gaudichaudia implexa* fruit morphology and geographic distribution of the holotype and paratypes. A–K, plants with ♀ ancestor from section *Gaudichaudia*: A) Jessup 4076 (type), B) Rzedowski 32522, C) Jessup 4079, D) Jessup 4080, E) Jessup 4081, F) Jessup 4082, G) Jessup 4037, H) Jessup 4018, I) Jessup 4100, J) Anderson 12624, K) Jessup 4105; L–X, plants with ♀ ancestor from section *Tritomopterys*: L) Jessup 4006, M) Jessup 4108, N) Anderson & Laskowski 3707, O) Jessup 4115, P) Anderson & Laskowski 4293, Q) Anderson & Laskowski 4056, R) Jessup 4002, S) Anderson 13316, T) Jessup 4000, U) Jessup 4001, V) Jessup 4113, W) Jessup 4114, X) Jessup 4106. Samara illustrations are approximately 1×.

distinctions will be difficult to discern. I collected flower buds of the type, prepared aceto-carmines squashes of meiotic pollen mother cells and counted the chromosomes. In three separate preparations I found  $n = 80$  pairs. Anderson (1993) reported chromosome counts in several collections included here as paratypes. Anderson found meiotic chromosome number was  $n = 80$  in Rzedowski 32522, Anderson & Laskowski 3707, Anderson & Laskowski 4056, Anderson & Laskowski 4293, Anderson 12624, and Anderson 13316.

**Paratypes.** Mexico. Plants with ♀ ancestor from section *Gaudichaudia*: Hidalgo: 7 km NE Mezquitlan, rd to Zacualtipan, 1800 m, 17 Nov 1974,

Rzedowski 32522 (MICH, IEB). Jalisco: Cerro Viejo, trail S of Tlajomulco, 1800 m, 5 Nov 1988, Jessup 4079 (CHAP, IEB, MICH, UC); 10 mi NE of Cocula, between Guadalajara and Autlán, 1380 m, 6 Nov 1988, Jessup 4080 (CHAP, IEB, MICH, UC); 10 mi NE of Cocula, between Guadalajara and Autlán, 1380 m, 6 Nov 1988, Jessup 4081 (CHAP, IEB, MICH, UC); 11.3 km NE of Tecolotlan, between Guadalajara and Autlán, 1480 m, 6 Nov 1988, Jessup 4082 (CHAP, IEB, MICH, UC). Michoacan: Mpio. Benito Juárez, 17.5 km S of Zitácuaro, 0.5 km S of Guanoro, 500 m, 16 Oct 1988, Jessup 4037 (CHAP, IEB, MICH, UC). Morelos: 1 km SE of Laureles village limit, Barranca Tezahu-

ate, ca. 3 km NW of Tlayacapan, 1800 m, 6 Oct 1988, *Jessup 4018* (CHAP, IEB, MICH, UC). Sonora: 18 km N of Yécora—Hermosillo hwy, on rd to Sahuaripa, 850 m, 12 Sep 1990, *Jessup 4100* (CHAP, IEB, MICH, UC). Zacatecas: 21 km S of Villanueva on rd to Jalpa, 1900 m, 12 Sep 1983, *Anderson 12624* (MICH); 21 km S of Villa Nueva, 1900 m, 16 Sep 1990, *Jessup 4105* (CHAP, IEB, MICH, UC). Plants with ♀ ancestor from section *Tritomopterys*: Guanajuato: 16 km NE of San Felipe, 1890 m, 2 Oct 1988, *Jessup 4006* (CHAP, IEB, MICH, UC); 19 km E of San Luis de la Paz on rd to Victoria, 2070 m, 17 Sep 1990, *Jessup 4108* (CHAP, IEB, MICH, UC). Jalisco: 9.7 km E of Villa Corona, above Lago Atotonilco, 1420 m, 24 September 1966, *Anderson & Laskowski 3707* (MICH). Nuevo Leon: 6.1 km S of Allende, between Linares and Monterrey, 10 Oct 1990, *Jessup 4115* (CHAP, IEB, MICH, UC). Oaxaca: 7.4 km NE of Chazumba, 2150 m, 23 Nov 1966, *Anderson & Laskowski 4293* (MICH). San Luis Potosí: 32.9 km W of Cd Valles, 485 m, 18 Oct 1966, *Anderson & Laskowski 4056* (MICH); 3.2 km W of Ciudad Valles, 420 m, 1 Oct 1988, *Jessup 4002* (CHAP, IEB, MICH, UC); 20 km E of Santa Catarina, 1200 m, 29 Oct 1983, *Anderson 13316* (MICH). Tamaulipas: hwy 101, 1.6 km S of bridge over Rio San Marcos, 14.5 km S of jct with hwy 85, 30 Sep 1988, *Jessup 4000* (CHAP, IEB, MICH, UC); 6.4 km N of jct hwy 85 and hwy 40, N of Guayalejo, 750 m, 1 Oct 1988, *Jessup 4001* (CHAP, IEB, MICH, UC); NW of Tampico, 4.8 km E of González, 8 Oct 1990, *Jessup 4113* (CHAP, IEB, MICH, UC); 77 km N of Ciudad Victoria, 32 km N Rio Purificación, 250 m, 8 Oct 1990, *Jessup 4114* (CHAP, IEB, MICH, UC). Zacatecas: Mpio. Jalpa, 5.1 km E of jct hwy 54 and hwy 70, rd to Aguascalientes, 16 Sep 1990, *Jessup 4106* (CHAP, IEB, MICH, UC).

*Gaudichaudia implexa* is morphologically more variable and geographically more widespread than any other species in *Gaudichaudia*. The name, which means “entangled,” refers not only to the typical habit of the plant in relation to the surrounding supportive, often spiny, prickly or thorny vegetation, but to the fact that lineages within this species represent the entangled accretion of genetically intertwining amphiploid lineages formed among diploid species in the *G. albida* sens. lat. and the *G. cynanchoides* sens. lat. complexes. All of the lineages in this species proliferate via autogamously produced samaras, exhibit samara wing morphology with some degree of shape intergradation among shapes typically found in the diploids, and on analysis of cpDNA exhibit a chloroplast haplotype typical of either the *G. albida* species complex or the *G. cynanchoides* species complex (Jessup 1994, 2002). Judging from the spectrum of samara wing morphology, the broad range of stem and leaf vestiture, and the combination of cpDNA haplotypes found it seems likely that more than one of the species in section *Tritomopterys* (Fig. 1) is active

in formation of the amphiploids. Ten cpDNA haplotypes were detected in samples representing section *Tritomopterys*, and twelve of the *G. implexa* collections (paratypes) shared one of those haplotypes with three species in section *Tritomopterys* (*G. albida*, *G. diandra*, *Gaudichaudia* sp. ined. “*intermedia*”). One additional haplotype closely related to other haplotypes carried by species in section *Tritomopterys* (*Gaudichaudia* sp. ined. “*velutina*,” *Gaudichaudia* sp. ined. “*intermedia*,” and *G. diandra*) was detected in a single collection of *G. implexa*. Of the eight cpDNA haplotypes detected in samples representing section *Gaudichaudia*, eight of the *G. implexa* collections shared one of those haplotypes with *G. cynanchoides*. Three additional haplotypes carried by specimens representing section *Gaudichaudia* were each detected in one collection of *G. implexa*.

The plants are typically found in ruderal habitats and range in geographic distribution (Fig. 6) from southern Puebla westward through the Eje Volcánico Transversal to central Jalisco, northward on the Altiplano Mexicano to Nuevo Leon, in scattered locations in the Sierra Madre Occidental, and eastward into the Sierra Madre Oriental in Tamaulipas, San Luis Potosí, Querétaro, and Hidalgo. Anomalous collections from Chihuahua, Coahuila and Durango probably represent rare isolated lineages of this species, similar to the northern disjunct population sampled from southeastern Sonora. Though formed as amphiploids among lineages in section *Tritomopterys* and section *Gaudichaudia*, the geographic range and apparent ecological amplitude of *G. implexa* far exceeds that of either ancestral diploid lineage.

Nothosection ***Zygotomopterys*** S. L. Jessup nothosect. nov. (*Gaudichaudia* sect. *Tritomopterys* × *Gaudichaudia* sect. *Zygopterys*), Fig. 7. This nothosection contains two amphiploid species from southern Puebla and west-central Oaxaca, with an isolated population of one species from central Guerrero.

***Gaudichaudia zygoptera*** S. L. Jessup, sp. nov. (Fig. 7)—TYPE: Mexico. Oaxaca: 10.1 km N of hwy 190 on rd to Guelatao, 1880 m, in thicket near stream, 22 Oct 1988, *Jessup 4042* (Holotype MICH; isotypes CHAP, IEB, UC).

A *Gaudichaudia galeottiana* facile distinguenda lobis lateralibus alae samarae valde asymmetricis, uno vel utroque lobo majori [quam eis *Gaudichaudia galeottiana*], lobo postico angustiori, et nulla constrictione lobi postici ad nucem, vel aliquot his differentiis. A formis *Gaudichaudia implexa* lobum posticum alae samarae latum ferentibus distinguenda apicibus loborum lateralium alae samarae late rotundatis pro apicibus obtuse acutis *Gaudichaudia implexa*.

Readily distinguished from *G. galeottiana* by a marked asymmetry in the lateral lobes of the sa-



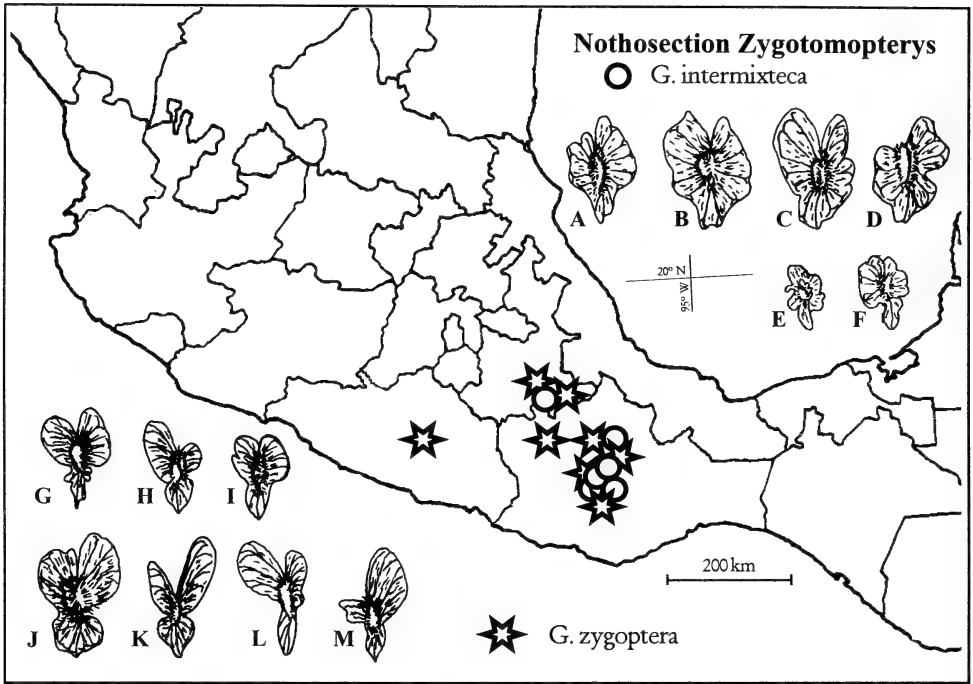


FIG. 7. Nothosection *Zygotompterys* fruit morphology and geographic distribution of the holotypes and paratypes. A–F, *G. intermixteca*: A) Jessup 4040, B) Anderson 13031, C) Jessup 4043, D) Jessup 4047 (type), E) Jessup 4046, F) Jessup 4045; g–m, *G. zygotera*: G) Anderson 12990, H) Jessup 4044, I) Jessup 4038, J) Jessup 4072, K) Jessup 4042 (type), L) Jessup 4049, M) Anderson 13138. Samara illustrations are approximately 1×.

mara wing, by one or both lobes larger than those found in *G. galeottiana*, by a narrower postical lobe of the samara wing, and by the absence of a prominent constriction in the postical lobe where it attaches to the nut, or by some combination of these features. Distinguished from phases of *G. implexa* that bear a broadened postical lobe of the samara wing by the broadly rounded apices on the lateral lobes of the samara wing, in contrast with the generally bluntly acute apices typical of the lateral lobes in *G. implexa*.

**Paratypes.** Mexico. Guerrero: 103 km N of Acapulco on rd to Chilpancingo, 8 km along rd to El Alquitran, 2000 m, 30 Oct 1988, Jessup 4072 (CHAP, IEB, MICH, UC). Oaxaca: 22.5 km S of Huahuapan on rd to Oaxaca, 2100 m, 20 Oct 1988, Jessup 4049 (CHAP, IEB, MICH, UC); Mpio. Oaxaca, vicinity of Monte Albán, 21 Oct 1988, Jessup 4044 (CHAP, IEB, MICH, UC). Puebla: .8 km NW of Cacaloapan on rd between Puebla and Tehuacan, 1970 m, 19 Oct 1988, Jessup 4038 (CHAP, IEB, MICH, UC); 89 km S of Teotitlan on rd to Oaxaca, 1500 m, 10 Oct 1983, Anderson 12990 (MICH); 3 km S of Ocotlan on rd from Oaxaca to Puerto Angel, 1540 m, 15 Oct 1983, Anderson 13138 (MICH).

Plants of ruderal habitat ranging from central and southern Puebla south into central Oaxaca (Fig. 7).

The name refers to the zygomorphy evident in the lobes of the lateral samara wing, which indicates the influence of ancestral hybridization with lineages from section *Tritompterys*. Though the evidence is weak for the branching order of sections, in the maximum likelihood analysis of cpDNA restriction sites section *Zygoterys* and section *Tritompterys* form a monophyletic group with section *Tritompterys* haplotypes forming a crown cluster, indicating possible paraphyly of section *Zygoterys*. All but one of the specimens of *G. zygoterys* sampled for cpDNA haplotypes carry haplotypes closely related to that carried by *G. galeottiana*, indicating that most of the hybridization contributing to the formation of this species involves pollen donors from section *Tritompterys*. The paratype Anderson 12990 has  $n = 80$  chromosome pairs at meiosis (Anderson 1993).

Only one of the cpDNA haplotypes encompassed in section *Zygoterys* is unequivocally assigned to *G. galeottiana*. The other haplotypes were found exclusively in *G. zygoterys*. The possibility remains that variation seen in samara morphology in *G. zygoterys* is indicative of relictualism, representing a tendency toward increased zygomorphy in the samara wing that persists in lineages that were ancestral to section *Tritompterys*. It seems more probable, however, that cpDNA haplotype di-



versity in section *Zygopterys* is indicative of ancestral diversity within *G. galeottiana* that has been swamped by introgression with adventive lineages from section *Tritomopterys*. One population of *G. zygoptera*, the western disjunct in central Guerrero, carries a cpDNA haplotype shared with three lineages (*G. albida*, *G. diandra*, *Gaudichaudia* sp. ined. "intermedia") within section *Tritomopterys*. An anomalous plant collected in southern San Luis Potosí (Anderson & Laskowski 4043) that is morphologically well placed in *G. implexa* bears a cpDNA haplotype from section *Zygopterys*. That plant, growing 500 km north of the range of *G. zygoptera*, is probably a hybrid between *G. zygoptera* and either *G. cynanchoides* or *G. implexa*. The nuclear DNA signature, based on randomly amplified DNA, places it close to *G. implexa*, nested close to *G. cynanchoides* (Jessup 1994).

***Gaudichaudia intermixteca*** S. L. Jessup, sp. nov. (Fig. 7)—TYPE: Mexico. Oaxaca: Mpio. Oaxaca, vicinity of Monte Albán, 21 October 1988, Jessup 4047 (Holotype MICH; isotypes CHAP, IEB, UC).

A stirpibus nothosectionis *Cyclotomopterys*, quibuscum generatim similis est forma alae samarae, distinguenda est lobo postico angustiori, apice lobi postici latiori minusque acuto-acuminata, lobis lateralibus vix ad valde asymmetricis, et samaris latioribus super centrum nucis, pro latioribus ad vel sub centrum nucis. A *Gaudichaudia synoptera* differt pilis caulibus minoribus adpressisque, non patentibus erectisve, brachiis trabeculae fere aequalibus in longitudine et numquam subaristatis ut frequenter in *Gaudichaudia synoptera*. *Gaudichaudia symplecta* similis indumento caulibus, sed pilis caulibus minoribus saepe pro ratione latioribus [quam eis *G. symplecta*]. Formae Oaxacae centralis alis samararum reductis a *Gaudichaudia cynanchoides* sedunt pilis parvis v-formibus omnino nullis.

Distinguished from lineages in nothosection *Cyclotomopterys*, with which it shares a general similarity in shape of the samara wing, by the narrower postical lobe of the samara wing, by the broader, less acute-acuminate apex of the postical lobe, by the slight to pronounced asymmetry in the lateral lobes of the samara wing, and in having the samaras typically widest above the center of the nut, rather than widest at or below the center of the nut. Differing from *G. synoptera* in having the stem hairs smaller and appressed rather than spreading or erect, with the limbs of the trabecula nearly equal in length and never subaristate as frequently found in *G. synoptera*. Somewhat similar in stem vestiture to *G. symplecta*, but with smaller stem hairs that are frequently wider relative to their length than those in *G. symplecta*. In phases from central Oaxaca with reduced samara wings, separable from *G. cynanchoides* by the complete absence of small v-shaped hairs.

**Paratypes.** Mexico. Oaxaca: 15 km W of Oaxaca on hwy 190, 1710 m, 11 Oct 1983, Anderson 13031 (MICH); Mpio. Oaxaca, vicinity of Monte Albán, 21 October 1988, Jessup 4043 (CHAP, IEB, MICH, UC); Mpio. Oaxaca, vicinity of Monte Albán, 21 October 1988, Jessup 4045 (CHAP, IEB, MICH, UC); Mpio. Oaxaca, vicinity of Monte Albán, 21 October 1988, Jessup 4046 (CHAP, IEB, MICH, UC); (CHAP, IEB, MICH, UC). Puebla: 8 km S and W of Tehuacan on rd to Huahuapan de Leon, 1900 m, Jessup 4040 (CHAP, IEB, MICH, UC).

*Gaudichaudia intermixteca* means "among the Mixtec," reflecting the narrow distribution of this species in central Oaxaca, where it is especially abundant and diverse in the vicinity of Monte Albán, but the name also denotes the genetically "intermixed" nature of this species. The species has clear affinities with lineages in section *Tritomopterys*, as shown by phylogenetic placement of the cpDNA haplotype borne by all collections examined. That cpDNA haplotype is, however, unique to *G. intermixteca*, suggesting an ancient hybridization that has persisted long enough to evolve a divergent genome. Nuclear DNA analysis places the group close to *G. galeottiana* and the *G. albida* complex (Jessup 2002). In addition to the concentration in the vicinity of Monte Albán, the species is found somewhat further north in Oaxaca and in extreme southern Puebla (Fig. 7). Anderson (1993) found  $n = 80$  pairs of meiotic chromosomes in the paratype Anderson 13031.

Nothosection ***Cyclotomopterys*** S. L. Jessup nothosect. nov. (*Gaudichaudia* sect. *Cyclopterys* × *Gaudichaudia* sect. *Tritomopterys*), Fig. 8. This nothosection includes two new species with restricted geographic ranges in the central and western Eje Volcánico Transversal.

***Gaudichaudia synoptera*** S. L. Jessup, sp. nov. (Fig. 8)—TYPE: Mexico. Edo. Mexico, Mpio. Tepetilixpa, 3.2 km S of Tepetilixpa on rd between Cuautla and Amecameca, 2160 m, 8 Oct 1988, Jessup 4020 (Holotype MICH; isotypes CHAP, IEB, UC).

A *Gaudichaudia symplecta* et *Gaudichaudia intermixteca* secedit pilis caulibus longis angustisque, erecto-patentibus ad subaristatis, numquam adpressis, caulibus hispidis, brachiis trabeculae inter se valde differentibus in longitudine. A *G. andersonii* differt samaris ovatis ad orbiculatis sine constrictione postica alae lateralis prope basin nucis.

Separable from *G. symplecta* and *G. intermixteca* by the relatively long and narrow stem hairs characterized by a marked difference in length of the trabecula limbs, the stem hairs erect-spreading to subaristate, never appressed, and the stems hispid. Distinct from *G. andersonii* in the ovate to orbicular samaras lacking a postical constriction in the lateral wing near the base of the nut.

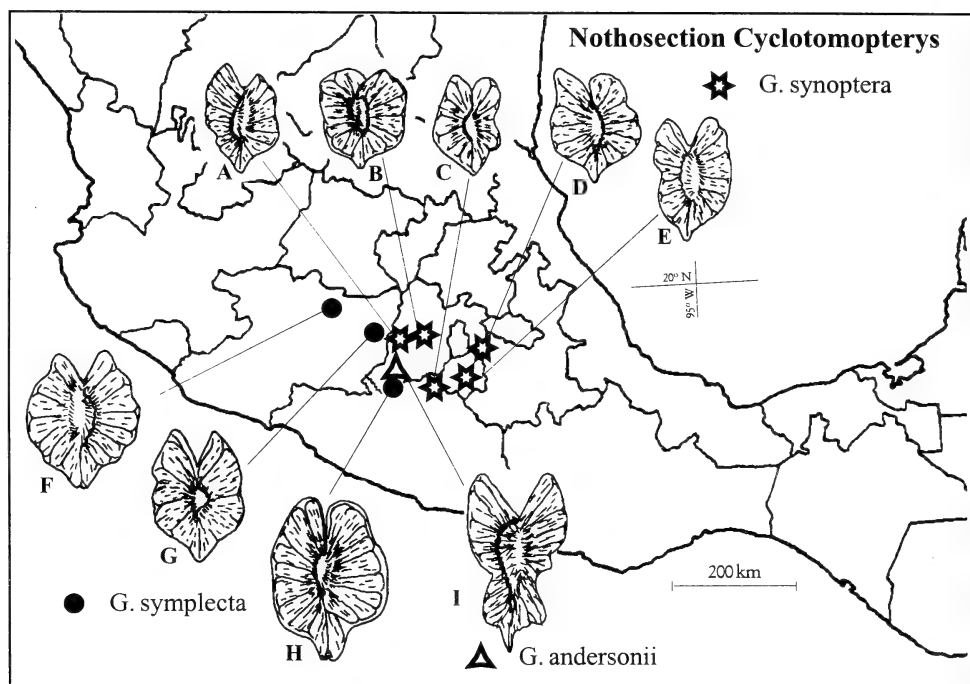


FIG. 8. Nothosection *Cyclotomopterys* fruit morphology and geographic distribution of the holotypes and paratypes. A–E, *G. synoptera*: A) Jessup 4022, B) Jessup 4023, C) Soto 4024, D) Jessup 4020 (type), E) Jessup 4015; F–H, *G. symplecta*: F) Jessup 4074 (type), G) Anderson 13291, H) Jessup 4025; I, *G. andersonii*: Jessup 4026 (type). Samara illustrations are approximately 1 $\times$ .

**Paratypes.** Mexico. Guerrero: Soto 4024 (MICH). Estado Mexico: 7 km W of Temascaltepec on rd to Real de Arriba, 2000 m, 10 Oct 1988, Jessup 4022 (CHAP, IEB, MICH, UC); 12 km SW of Temascaltepec on rd to Tejupilco, 1750 m, 11 Oct 1988, Jessup 4023 (CHAP, IEB, MICH, UC). Morelos: ca. 1 km SE of Laureles village limit, Barranca Tezahuatle, ca 3 km NW of Tlayacapan, 1800 m, 6 Oct 1988, Jessup 4015 (CHAP, IEB, MICH, UC).

*Gaudichaudia synoptera* is one of two recognizable hybrid species formed between species in section *Tritomopterys* and section *Cyclopterys*. It is immediately separable from the other species in this nothosection by the distinct morphology of stem hairs (Fig. 9). The most probable origin for *G. synoptera* is as an amphiploid between *Gaudichaudia* sp. ined. “*hirsuta*” and *G. cycloptera*. The evidence from morphology and DNA analyses supports that conclusion. The stem vestiture is similar

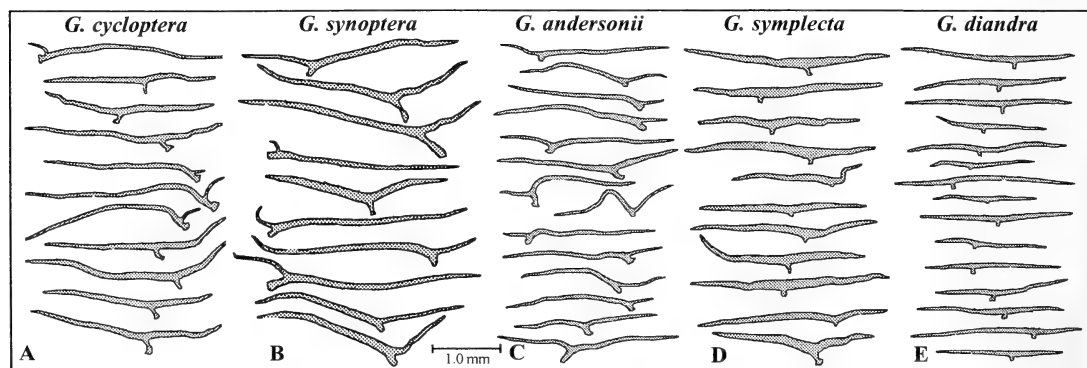


FIG. 9. Comparison of stem hairs on representative collections from Michoacan. A) *G. cycloptera*, Jessup 4033; B) *G. synoptera*, Jessup 4020 (type); C) *G. andersonii*, Jessup 4026 (type); D) *G. symplecta*, Jessup 4074 (type); E) *G. diandra*, Jessup 4034.

to that found in *Gaudichaudia* sp. ined. "*hirsuta*," and some of the collections tested share a cpDNA haplotype with members of that lineage. The type bears a cpDNA haplotype that, outside of the *G. synoptera* collections, is restricted to Oaxaca and Chiapas where it is most typically carried by *Gaudichaudia* sp. ined. "*hirsuta*" and *Gaudichaudia* sp. ined. "*velutina*" (Fig. 1).

Nuclear DNA analyses place the type closest to *Gaudichaudia* sp. ined. "*hirsuta*." Other members of the species carry a cpDNA haplotype that is most commonly carried by *G. cycloptera*. The name means "twining together," reflecting the tendency of several twining branches, even from different plants, and occasionally from different species, to form "limbs" by twining together. The obvious analogy is that the lineages themselves are intertwined in this species that apparently originated through hybridization of plants from different sections of *Gaudichaudia*. The literal meaning of the name and the metaphorical meaning coincide in this plant to the extent that the habit of forming twined limbs complexed from shoots of different genets facilitates wide outcrossing and a reticulated ancestry. The pollinators are anthophorine bees specialized for collecting oil from the calyx glands present as part of the conservative malpighiacean floral syndrome (Vogel 1974; Anderson 1990), and are adapted for the family-level floral characters. The bees likely do not distinguish among species within a genus, and are thus more apt to cross pollinate divergent lineages when the flowers are closely juxtaposed, as they often are in the tangled thickets inhabited by *Gaudichaudia*. *Gaudichaudia synoptera* has a rather narrow geographic distribution (Fig. 8), ranging from southwestern Edo. Mexico, where it is especially common in the vicinity of Temascaltepec, eastward into Morelos, and in Edo. Mexico east of Distrito Federal.

***Gaudichaudia symplecta*** S. L. Jessup, sp. nov. (Fig. 8) TYPE: Mexico. Michoacan, Mpio. Morelia, 23.5 km E of Morelia on rd from Cd Hidalgo, 2170 m, 1 Nov 1988, *Jessup 4074* (Holotype MICH; isotypes CHAP, IEB, UC).

A *Gaudichaudia cycloptera* secedit incisura apicali insigni alae lateralis et apice acuto-acuminata marginis posticae loborum lateralium alae. A *Gaudichaudia synoptera* et *Gaudichaudia andersonii* differt indumento caulis, pilis adpressis, numquam erecto-patentibus vel subaristatis, caulibus ita sericeis, non hispidis, brachiis trabeculae subaequalibus in longitudine. A *Gaudichaudia intermixteca* differt lobis alae lateralis samarae plerumque symmetricis et samaris latioribus ad vel sub medium.

Separable from *G. cycloptera* by the pronounced apical notch in the lateral wing, and the acute-acuminate apex of the postical margin of the lateral wing lobes. Distinct from *G. synoptera* and *G. andersonii* in the stem vesture, comprising hairs that

are subequal in length of the trabecula limbs, uniformly appressed, never erect-spreading or subaristate, the stems thus sericeous, not hispid. Differing from *G. intermixteca* in the generally symmetric lobes of the lateral samara wing, and in having the samaras widest at or below the middle.

**Paratypes.** Mexico. Estado Mexico: 0.5 km N of Amatepec on rd to Tejupilco, 1750 m, 11 Oct 1988, *Jessup 4025* (CHAP, IEB, MICH, UC). Michoacan: Mpio. Zitacuaro, Puerto del Gato, 5 km N of Zitacuaro on hwy 15, 1800 m, 26 Oct 1983, *Anderson 13291* (MICH).

The name means twisted and plaited together, referring to the habit, as in the previous species, of forming branches that appear almost braided from separate twining branches. Both the type and one of the paratypes (*Anderson 13291*) bear a cpDNA haplotype that is characteristic of section *Tritompterys*. The other paratype (*Jessup 4025*) bears a cpDNA haplotype that is otherwise confined to lineages within section *Cyclopterys*. Unlike its close relative, *G. synoptera*, this species has stem trichomes that are in all respects similar to those typically found in *G. albida* sens. str. Nuclear DNA analyses also place members of this species close to lineages within section *Cyclopterys*. The conclusion that *G. symplecta* originated as an amphiploid cross between *G. albida* and *G. cycloptera* is thus well supported.

Among the plethora of specific and infraspecific taxa treated by Niedenzu, none is a feasible candidate for assignment of this species. Niedenzu moved *G. arnottiana* Juss. to subspecific rank under *G. pentandra* Juss. (= *G. cycloptera* (DC.) W. R. Anderson) and described three new varieties and two new forms of *G. pentandra* subsp. *arnottiana* (Juss.) Niedenzu. One or more of those infraspecific names might be construed as referring to this species, but the characters Niedenzu emphasized in his diagnoses make it difficult to reach a conclusion about circumscription of his taxa. Jussieu (1843) clearly expressed doubt that his *G. arnottiana* is distinct from *G. cycloptera*: "admodum affinis praecedenti, cum qua staminibus quinque antheriferis aequalibus convenit foliorumque formam (fide iconis); calyce, ut videtur, 10-glanduloso ut quibusdam levioris momenti notis subdissimilis; forsân conjungenda. Species Candolleana forsân conspecifica, certè congener fide iconis Flor. Mexic. ined. in qua carpellum calyce eglanduloso stipatum pendere e filo videtur." The "closely related preceding species" is *G. cycloptera* (DC.) W. Anderson, and nothing in the protologue clearly differentiates *G. arnottiana* from *G. cycloptera* or indicates characters that would suggest the name should apply to the species that I am naming *G. symplecta*. Jussieu in fact expressed doubt that *G. arnottiana* is distinct and suggested that they are conspecific. Niedenzu's infraspecific elaborations notwithstanding, *G. ar-*

*nottiana* Juss. can be considered a synonym of *G. cycloptera* (DC.) W. R. Anderson.

**Gaudichaudia** (sect. *Cyclopterys*) **andersonii** S. L. Jessup, sp. nov. (Fig. 8)—TYPE: Mexico. Estado Mexico: 1 km S of Temascaltepec on rd to Tejupilco, 1790 m, 13 Oct 1988, *Jessup 4026* (Holotype MICH).

A speciebus aliis differt samaris magnis incisura apicali insigni alae lateralis, lobos duos laterales symmetricos sinu lata v-forma separatos formantibus, marginibus alae lateralis rotundatis et ad constrictionem sub centrum contractis, lobo postico expanso e constrictione sub nucem et interdum cauda brevi abrupta ornato.

Distinct from other species in the large samaras with pronounced apical notch in the lateral wing, forming two symmetric lateral lobes separated by a broad v-shaped sinus, the lateral wing margins rounded to a constriction in the wing below center, the postical lobe flared from the constriction below the nut and sometimes abruptly appended by a short tail.

*Paratype*. Mexico. Estado Mexico: 1.6 km S of Temascaltepec on Temascaltepec-Tejupilco-Amatepec rd, 1600 m, 14 Oct 1966, *Anderson & Lasowski 3988* (MICH).

This very distinctive species is named in honor of William R. Anderson who has devoted years of field and laboratory work to the study of *Gaudichaudia*, among other malpighs. I found the species during a prolonged foray in the tangled vegetation south of Temascaltepec, occasioned by mechanical failure of the VW microbus, belonging to S. D. Koch, in which Anderson and I were passengers during an expedition into northern Guerrero. Anderson had collected the species in 1966 in the same general area (Fig. 8). Nothing like it has been found anywhere else, and other than the type and paratype cited here, I am unaware of other collections of this species.

In vegetative characters and floral morphology *G. andersonii* resembles both *G. cycloptera* and *G. synoptera*. The long, rather narrow stem hairs with distinctly unequal limbs of the trabecula (Fig. 9) are a fairly close match to those found in *G. cycloptera*, but are somewhat smaller than those found in *G. synoptera*, and although the hairs are distinctly erect-spreading in *G. andersonii*, they do not form the distinctive subaristate stem vestiture found in *G. synoptera*. The type of *G. andersonii* was found to carry a cpDNA haplotype otherwise known only from a topotype collection of *G. chasei*. In the nuclear DNA analysis *G. andersonii* is closely placed with *G. cycloptera*, well apart from *G. chasei*, which is placed closer to *G. intermixteca* and *G. galeottiana* in that analysis (Jessup 1994). The molecular data suggests that *G. andersonii* is a hybrid within section *Cyclopterys* between *G. cycloptera* and *G. chasei*, and the intermediacy of sa-

mara wing morphology is consistent with that conclusion.

## DISCUSSION

Tribe Gaudichaudieae, as most recently defined (Anderson 1985) includes *Gaudichaudia*, *Aspicarpa*, *Janusia*, *Camarea*, and *Peregrina*. According to Davis et al. (2001), the tribe is well supported as a monophyletic group nested within a well supported monophyletic stigmaphylloid clade, which includes (in addition to Tribe Gaudichaudieae) *Stigmaphyllon* and *Banisteriopsis*, among other genera. A lineage resembling one of the stigmaphylloids is the most plausible ancestor for Tribe Gaudichaudieae. Examining the distribution of chromosome numbers (Anderson 1993) across the entire stigmaphylloid clade we see in species representing basal lineages a high frequency of  $n = 10$  meiotic chromosome pairs, probably the base number for the clade. In *Banisteriopsis* 13 of 14 species reported have  $n = 10$  pairs, and one has  $n = 20$  pairs. In *Stigmaphyllon* 4 of 4 species reported have  $n = 10$  pairs. Within Tribe Gaudichaudieae, ploidal levels in *Janusia* are  $n = 10$  (2 of 12 species reported),  $n = 20$  or, in one case, aneuploid  $n = 19$  (9 of 12 species reported), and  $n = 40$  (1 of 12 species reported). Chromosome numbers in *Aspicarpa* are  $n = 20$  (1 of 6 species reported) and  $n = 40$  (5 of 6 species reported). *Camarea* all have  $n = 17$ , and *Peregrina* has  $n = 19$  meiotic pairs. In *Gaudichaudia* chromosome number is  $n = 40$  or  $n = 80$  (and  $n = 120$  in one isolated collection).

The chromosome numbers in combination with the molecular data strongly support the hypothesis that evolution in the stigmaphylloids has proceeded by a series of genomic doublings trending from  $n = 10$  to  $n = 80$ , producing a polyploid series on the base number  $x = 10$ . In the stigmaphylloid clade, *Banisteriopsis* and *Stigmaphyllon* are ancestral diploids, with a single tetraploid in *Banisteriopsis*. *Janusia* is primarily tetraploid with two diploid lineages remaining and a single octoploid lineage. *Camarea* and *Peregrina* are most likely aneuploid reductions from the tetraploid state. *Aspicarpa* is now understood to be at least in part nested within *Gaudichaudia* and retains a single known tetraploid lineage, but is primarily octaploid. *Gaudichaudia* sensu stricto is fundamentally octoploid, but developed a series of wide crosses at the sextodecaploid level, including the species described in this paper.

The genus *Gaudichaudia* is apparently built on an ancient polyploid complex. Regular meiotic pairing among homologous chromosomes resulted in essentially instantaneous diploidization of amphiploid crosses. Since the trend toward higher ploidy is clearly demonstrated within the stigmaphylloid clade, the obvious hypothesis is that lineages with lower ploidy will be phylogenetically more basal within Tribe Gaudichaudieae. If that hy-

pothesis is supported by molecular phylogenetic tests, I predict that relict lineages will be found to exist within *Gaudichaudia*, perhaps as narrow endemics or isolated populations in central Mexico, that retain the primitive lower ploidal levels. The occurrence of such lineages is already a strong possibility within section *Oligopterys*, since a single species of *Aspicarpa* (*A. schinnii* W. R. Anderson) is known to retain the  $n = 20$  condition (Anderson 1993). That species may or may not properly belong within *Gaudichaudia*, and it remains to be seen whether molecular data will place that lineage as basal within the section. A thorough screening of isolated lineages within other sections of *Gaudichaudia* is likely to reveal additional instances if indeed any are extant.

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RETICULATE ANCESTRY IN MEXICAN *GAUDICHAUDIA*  
(MALPIGHIACEAE) ANALYZED WITH RAPD's AND  
SOUTHERN HYBRIDIZATION

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ABSTRACT

Evidence of relationships based on randomly amplified polymorphic DNA (RAPD) data combined with information about cpDNA haplotypes can be used to resolve details of reticulate ancestry in an otherwise intractable polyploid complex in *Gaudichaudia* (Malpighiaceae). Robust inference of genetic relationships among taxa, however, depends critically on two assumptions: (1) character states compared among taxa are homologous, and (2) characters scored as different are independent. Application of randomly amplified DNA methods, such as RAPD's, have largely made these assumptions without testing them. In this study I use RAPD's to elucidate relationships among lineages and to infer reticulate ancestry of amphiploid lineages in *Gaudichaudia*. I test the assumption that comigrating RAPD fragments are homologous using hybridization of radio-labeled RAPD fragments probed against blots of randomly amplified DNA as an indicator of homology. The probes bind strongly only to fragments on the blots having sequence homology. Results demonstrate that all gel fragments included in the analysis meet the assumption of homology. Gel fragments can therefore be reliably scored directly as characters. The assumption of independence of RAPD fragments is also explored. Although multiple fragments with strong sequence homology appear in most blots, gel-visualized fragments are generally independent.

RESUMEN

La evidencia de relaciones basadas en datos de DNA polimórfico aleatoriamente amplificado (RAPD) combinados con información sobre haplotipos cpDNA se puede utilizar para resolver detalles, de otra manera insuperables, de ascendencia reticulada en un complejo poliploide en *Gaudichaudia* (Malpighiaceae). La sólida inferencia de relaciones genéticas entre especies, sin embargo, depende críticamente de dos supuestos: (1) los estados del carácter comparados entre grupos taxonómicos son homólogos, y (2) los caracteres anotados como diferentes son independientes. El uso de los métodos de DNA amplificado aleatoriamente, tales como los RAPD's, ha hecho estas asunciones en gran parte sin probarlas. En este estudio utilizo RAPD's para aclarar relaciones entre linajes y para deducir la ascendencia del reticulado de linajes de anfiploides en *Gaudichaudia*. Pongo a prueba la asunción de que los fragmentos comigrantes de RAPD son homólogos usando la hibridación de fragmentos RAPD marcados radiactivamente como testigos contra manchas de DNA aleatoriamente amplificado como un indicador de la homología. Los testigos se adhieren fuertemente solamente a aquellos fragmentos dentro de las manchas que tienen homología de secuencia. Los resultados demuestran que todos los fragmentos del gel incluidos en el análisis cumplen con la asunción de la homología. Los fragmentos de gel se pueden por lo tanto contar confiablemente directamente como caracteres. También se explora la asunción de independencia de los fragmentos de RAPD. Aunque los fragmentos múltiples con fuerte homología de secuencia aparecen en la mayoría de las manchas, los fragmentos gel-visualizados son generalmente independientes.

Key Words: Polyploid, introgression, Malpighiaceae, RAPD, Southern hybridization.

*Gaudichaudia* (Malpighiaceae) has been revised based in part on inference from patterns of variation in cpDNA restriction sites (Jessup 2002). Evidence of relationships among lineages within *Gaudichaudia* from morphology, chromosome counts, and amplification of RAPD fragments corroborates the cpDNA evidence and helps to further resolve reticulate ancestry of some species in the genus (Jessup, 1994). In particular, a minimum spanning tree analysis of RAPD fragments (based on presence of amplified fragments visible on agarose gels), constructed using Jaccard similarity, shows broad congruence of cpDNA haplotypes and nuclear genomes. Plants that were inferred to be intersectional amphiploids, based on morphological features and

chromosome numbers, showed combinations of cpDNA haplotypes and nuclear genomes characterized by RAPD profiles that supported the hybridity hypotheses.

While the RAPD data helps define lineages and clearly demonstrates patterns of relationship and ancestry among the lineages, a test of the validity of the underlying assumptions about the RAPD data nevertheless remains worthwhile (Arnold and Emms 1998; Rieseberg 1996; Wolfe and Liston 1998), especially since gel fragments alone might be useful for inferring relationships. Homology of character states and independence of characters are prerequisite features of characters used in many systematic analyses. Restriction fragments are

strongly correlated, which is why restriction fragments alone cannot be scored for presence/absence and used directly as characters. While randomly amplified DNA markers, such as RAPD's, have not been shown to be correlated in the same way that restriction fragments are, estimates of relationship based on RAPD fragments would be similarly skewed if tightly linked markers were treated as independent estimators of relatedness (Lynch 1988). Estimates of relatedness would also be inaccurate if fragments of the same electrophoretic mobility were commonly of heterologous origins. In this paper I present the results of the RAPD analysis in *Gaudichaudia* and report experiments that test RAPD band homology and independence using hybridization of  $^{32}\text{P}$  labeled RAPD probes to southern blots of RAPD gels. I demonstrate the utility of the procedure in identifying the specific ancestry of amphiploids. When combined with knowledge of cpDNA haplotypes in the samples, this procedure further resolves reticulate ancestry by specifying which of the parental lineages contributed the maternal genome.

*Expected behavior of RAPD markers in amphiploids.* In tetraploid *Gaudichaudia* where chromosomes from divergent lineages may reside within the same nucleus, and where the lineages are reproducing primarily by selfing (Anderson, 1980), markers that occur within the same set of chromosomes can be tightly linked. When homeologous chromosome sets are divergent but still pair at meiosis in wide amphiploid crosses, we expect a marked reduction in viable gametes and reduced fecundity in the  $F_1$  progeny. Given that strongly inbreeding lineages quickly approach fixation of variable alleles (Li 1976), it seems likely that a preponderance of markers will frequently be fixed within a set of chromosomes in strongly selfing lineages. With little or no recombination between homeologous chromosomes most variability occurs among rather than within homeologous sets of chromosomes. Lineages with size variants of the same marker fixed on different (homeologous) sets of chromosomes—synologous loci as defined by Mindell & Meyer (2001)—will exhibit fixed heterozygosity. The variants that occurred in the ancestral diploids as orthologous loci, as fixed differences at the same locus in different lineages, are combined in the amphiploid as synologous loci, though they are less likely to be fixed in progeny resulting from outcrossing. Since RAPD sites are restricted to individual chromosomes, they necessarily obey all of the constraints associated with chromosomal inheritance.

We expect that RAPD fragments of the same molecular weight—fragments that appear at precisely the same location on a gel—are products of homologous sites. There is, however, the possibility of heterologous fragments with the same mobility—fragments that are identical in state but not ho-

mologous. We also expect that fragments of different mobility are independent products of unlinked sites. The assumptions of homology and independence, then, can be reduced to two questions. (1) Is there sequence homology among bands of different electrophoretic mobility within a sample? If we count multiple bands as distinct when they are in fact the result of a single locus then we violate the assumption of independence. (2) Is there sequence homology among bands of the same electrophoretic mobility among samples? If we count bands of the same electrophoretic mobility as identical when they are in fact distinct then we violate the assumption of homology. Testing those assumptions is simple in principle. An estimate of sequence homology can be obtained by observing the relative strength of hybridization signal between a labeled RAPD probe of known origin and samples from bands of the same molecular weight whose homology is in question. Bands that hybridize strongly to the probe are inferred to have a high level of sequence homology with the probe. By inference, a strong hybridization signal is an indicator of close relatedness.

#### MATERIALS AND METHODS

*DNA extraction.* Plants in the genus *Gaudichaudia* were sampled from a wide geographic area in Mexico, representing the center of diversity in the genus. Detailed source data for the collections is reported elsewhere (Jessup, 1994). Total genomic DNA was extracted from leaves that were snap-frozen in liquid nitrogen and subsequently stored at  $-80^\circ\text{C}$ . Total genomic DNA extraction was based on the CTAB procedure presented by Hillis et al. (1990) and Dowling et al. (1996). All DNA extractions were purified by ultracentrifugation on cesium chloride gradients, dialysis to remove the cesium chloride, and ethanol precipitation following procedure in Sambrook et al. (1989). Final yield of DNA was between 25 and 750  $\mu\text{g}$  DNA per extraction (from 1–2 grams of leaf tissue). In all, 134 different DNAs were successfully prepared for use in the molecular procedures. DNA concentrations and estimates of DNA purity were calculated from optical density measurements at  $\lambda = 260$ ,  $\lambda = 280$ , and  $\lambda = 320$  nm, on a Beckman DU-64 UV spectrophotometer.

*RAPD reactions and Southern hybridization.* Purified template DNA was diluted to 1 ng/ml in a reaction elixir buffered to pH 8.3 with 10 mM Tris-HCl containing 50 mM KCl, 2 mM  $\text{MgCl}_2$ , dNTPs at a concentration of 100  $\mu\text{M}$  each, five arbitrary 10-base oligonucleotide primers (Operon®) were used in separate reactions, each at a concentration of 0.2  $\mu\text{M}$ , and Taq DNA polymerase (Perkin Elmer®) was used in all reactions at a concentration of 0.07 units/ng template DNA. The reaction was carried out in a total volume of 25  $\mu\text{l}$  on an M.J.Research® thermal cycler programmed at max-



imum ramp speed for: 1 cycle of 30 seconds at 94°C; 45 cycles of 1 minute at 94°C, 1 minute at 35°C, and 2 minutes at 72°C; and 1 cycle of 5 minutes at 72°C, followed by a hold at 4°C.

The products of the PCR reactions were separated by electrophoresis on 2% agarose gels with 200 ng/ml ethidium bromide, at 25V constant voltage for approximately 14 hours at room temperature in 1× TAE, pH 7.6. A 100-bp ladder (Pharmacia Biotech®) was loaded into three or four lanes on each gel at even intervals among samples as a high resolution molecular weight marker. Each gel run contained from 120 to 134 sample lanes and 12–16 molecular weight marker lanes over four gels. RAPD fragments were visualized by UV transillumination, then photographed on Polaroid-57 at f8, 3' 20". Negatives were washed in NaSO<sub>3</sub> 18% for 1 minute, then rinsed 30 minutes in H<sub>2</sub>O. RAPD fragments visible on the negatives were scored by careful measurement on a lightbox, and molecular weights were determined with the gel analysis program, Gel Match™ (UVP). All visually detectable fragments on either the films or the scanned images were scored as present. Computer image enhancement was used to intensify faint bands. Lanes not showing a fragment at the same position on the gel were scored as absent.

RAPD fragments from the PCR reactions were collected from ethidium bromide stained gels under UV transillumination. Bands selected for <sup>32</sup>P labeling were sampled by inserting the tip of a pasteur pipet into the center of the band and applying light vacuum pressure with a pipet pump as the tip was withdrawn from the gel. This produced a cylindrical gel section about 1 mm wide by about 7 mm long while preserving the source gel for blotting. The gel section was extruded into a microfuge tube and kept on ice. Collected fragments were diluted 10:1, reamplified using the original PCR protocol, then electrophoresed on 3% low T<sub>M</sub> agarose gels to further purify the fragment.

The whole reamplified fragment was collected after gel purification and 12 µl was radio-labeled with α-<sup>32</sup>P tagged ATP using a polymerase reaction. A few ng of molecular weight marker were also labeled at the same time as the RAPD probes. Labeling reactions were carried out using random priming with a mixture of hexadeoxyribonucleotides (6 bp oligonucleotides) according to the protocol developed by Feinberg and Vogelstein (1983, 1984). This technique resulted in probes labeled to high specific activity. Unincorporated nucleotides were separated from labeled RAPD fragments using sephadex columns set up in 9" glass pasteur capillary pipettes. Purified labeled probe was denatured by immersion in boiling water for 10 minutes, then 'quenched' on ice for 3–5 minutes before beginning the membrane hybridization reaction.

RAPD gels were blotted to nylon (Zetabind®) membranes following procedures in Maniatis et al. (1989). Membranes were allowed to dry after trans-

fer of the amplified fragments then stored at room temperature until Southern hybridization.

Prehybridization and Southern hybridization reactions followed procedure outlined in Dowling et al. (1996). The prehybridization solution was 4× SSC, 1% SDS, and 0.5% nonfat dry milk. Blots which had not been previously probed were first pretreated by washing in 0.1× SSC, 0.5% SDS for 1 hour at 65°C. Prehybridized blots were removed from the incubator and all but about 15 ml of the prehybridization solution was removed from the hybridization tray. The labeled probe was then added to the tray and thoroughly mixed. Several blots were hybridized simultaneously. Care was taken not to introduce bubbles into the space between blots. Hybridization reactions were allowed to proceed for 12–18 hours at 62°C.

Hybridized blots were removed from the trays and washed in three or four changes of 2× SSC, 0.5% SDS: two short washes at room temperature followed by one or two 30–45 minute washes at 60°C. Blots and discarded wash were monitored with a Geiger counter during the wash procedure to assess when background radiation on the filters had been adequately reduced. Filters were removed from the final wash and blotted to remove excess wash, then wrapped in plastic and placed in x-ray film cassettes with intensifying screens. Kodak X-OMAT™ AR film was loaded into the cassettes and they were exposed over night at –85°C. Films were removed and developed on an X-OMAT™ automatic X-ray film developer. Following autoradiography, blots were stripped of probe in hot 0.5× SSC and monitored until radiation was reduced to low levels. Blots were then prepared for reprobing with a different RAPD fragment.

## RESULTS

*Relationships inferred from RAPD fragments.* Seventy-five plants were scored for 79 RAPD sites. Table 1 records the molecular weights of RAPD fragments scored from the gels for each of the primers used in the study. Table 2 records the fragments scored from the gels for each collection. Usable sites were those that could be consistently scored for all 75 collections included in the analysis. Figure 1 shows a typical RAPD gel, in this case with RAPD bands produced using primer sequence CAAACGTCGG (A-19). Collections are arrayed on the gels by taxon defined on morphological similarity, and within taxon by geographic region. There are four marker lanes per gel, each a 100 bp ladder with molecular weight indicated for the 800 bp fragments. Blank lanes are collections that did not amplify. Blank lanes are excluded from the data tables. Notice the general pattern of shared bands. Bands of the same molecular weight tend to occur in adjacent lanes on the gel, i.e., among collections grouped by taxon and geographic proximity.

The data were clustered with a minimum spanning



TABLE 1. RAPD FRAGMENTS AMPLIFIED FROM 76 COLLECTIONS. Size of each fragment (kb) is reported for six different primers used in the analysis. Column numbers refer to the data matrix (Table 2).

Column Primer	1-16 A-9	17-31 A-10	32-34 A-15	45-49 A-16	50-62 A-18	63-79 A-19
	1.85	2.28	2.80	3.50	1.95	3.70
	1.75	2.15	1.90	2.00	1.70	3.50
	1.65	2.00	1.80	1.90	1.60	2.50
	1.55	1.65	1.60	1.40	1.53	2.20
	1.45	1.60	1.50	1.30	1.43	1.90
	1.35	1.50	1.35		1.40	1.70
	1.30	1.30	1.25		1.38	1.50
	1.25	1.20	1.20		1.35	1.48
	1.20	1.18	1.10		1.28	1.45
	1.15	1.15	1.00		1.20	1.43
	1.05	0.95	0.90		1.15	1.40
	0.95	0.85	0.80		1.00	1.38
	0.85	0.70	0.75		0.90	1.30
	0.80	0.65			1.20	
	0.70	0.60			1.10	
	0.60				0.90	
					0.85	

tree using the program Minspan (Podani 1993). A minimum spanning tree is the branching graph of OTU-wise association coefficients that minimizes the sum of all edges. Minimum spanning trees were computed for the RAPD data using the coefficient of Jaccard (Sneath and Sokal 1973), which does not include negative matches as a component of similarity (or dissimilarity). This is necessary when estimating relationships from randomly amplified DNA data since absence of a site does not convey any useful information about relatedness. Many distantly related OTU's will have state 0 for a large number of sites. Most of those characters, identical in state, will not be identical by descent. The RAPD minimum spanning tree is plotted (Figs. 2-4) and mapped with representative fruits from plants bearing each of the cpDNA haplotype defined in Jessup (2002). Each plant included in the analysis is designated with an OTU number in the diagrams corresponding to a row in Table 1.

*Correspondence of cpDNA haplotypes and RAPD's.* The longest span in the tree falls between OTU 3 and OTU 5, and effectively defines a left and right half of the minimum spanning tree. cpDNA haplotypes from section *Tritomopterys* map in part to each side of the minimum spanning tree (Fig. 2). Most plants bearing cpDNA haplotypes from section *Tritomopterys* with asymmetric fruit wings map to the right half of the tree. All but one plant (OTU 5) bearing cpDNA haplotypes from section *Tritomopterys* that map to the left side of the tree have irregular or intermediate fruit wing symmetry and belong to *G. implexa* Jessup (nothosection *Tritomochaudia*). Plants bearing cpDNA haplotype D (OTU's 64, 66, and 76) or cpDNA

haplotype B (OTU 59) having large symmetric fruit wings typical of *G. cycloptera* (DC.) W. R. Anderson map in a cluster far to the right with plants from section *Tritomopterys* and are all members of nothosection *Cyclotomopterys*, either *G. synoptera* Jessup (OTU's 59 and 66) or *G. symplecta* Jessup (OTU's 64 and 76). Plants with asymmetric fruit wings bearing cpDNA haplotype D (OTU's 2, 3, 6, 8, 18) are all members of section *Tritomopterys* and map just to the right of the span separating the two halves of the spanning tree.

Plants with cpDNA haplotypes from section *Cyclopterys* (OTU's 21, 59, 61) map to the same area on the minimum spanning tree as those with similar fruits bearing cpDNA haplotypes from section *Tritomopterys* (Fig. 4). Plants in *G. mcvaughii* W. R. Anderson, however, map to the far left (OTU's 22 and 23), even though they carry cpDNA haplotypes that clearly place them in section *Cyclopterys* (Fig. 4). In particular, OTU 21 (in *G. cycloptera*), far right, and OTU 23 (in *G. mcvaughii*), far left, both bear cpDNA haplotype AB from section *Cyclopterys*. One plant with morphology of *G. cycloptera*, and bearing a cpDNA haplotype from section *Cyclopterys* (OTU 19), maps closer to the asymmetric-winged plants bearing section *Tritomopterys* cpDNA haplotypes.

Plants bearing section *Gaudichaudia* cpDNA haplotypes all map on the left side of the RAPD minimum spanning tree (Fig. 3). One plant bearing a section *Gaudichaudia* cpDNA haplotype but with fruit wing morphology similar to *G. cycloptera* or *G. mcvaughii*, maps to the far left close to the position of *G. mcvaughii*. Several plants having intermediate fruits and carrying section *Gaudichaudia* cpDNA haplotypes (Fig. 3) map just to the left of center (OTU's 52, 67, 68, 69, 70, 71, 75). Plants with similarly intermediate fruit wing shapes but carrying section *Tritomopterys* cpDNA haplotypes map in the same region on the RAPD tree (OTU's 25, 53, 54, 55, 56, 58, 65, 72). All of the plants with intermediate fruit wing morphology mapping to this region of the minimum spanning tree are *G. implexa* Jessup in nothosection *Tritomochaudia*. Plants with morphology typical of *G. cynanchoides* H. B. K. map near the center of the left half of the tree (OTU's 40, 41, 42, 44, 45, 46, 47, 48). Three plants with intermediate fruits map to the far left, one bears section *Tritomopterys* cpDNA haplotype L (OTU 50), and the other two bear section *Gaudichaudia* cpDNA haplotype S (OTU's 49, 51). Those plants are also *G. implexa*.

Plants in *G. galeottiana* (Nied.) Chodat, or with fruit morphology approaching that of *G. galeottiana*, and bearing section *Zygopterys* cpDNA haplotypes (Fig. 4) cluster together on the RAPD tree on one long branch just to the right of center (OTU's 27, 28, 29). Plants in that cluster with slightly asymmetric wings are *G. zygoptera* Jessup (OTU's 28 and 29) or *G. intermixteca* Jessup (OTU 26) in nothosection *Zygotomopterys*. Only one

TABLE 2. PRESENCE/ABSENCE OF RAPD SITES IN EACH OF THE 75 SPECIMENS USED IN CALCULATION OF THE MINIMUM SPANNING TREE. Sites are listed in Table 5.

State	Accession	OTU	1	10	20	30	40	50	60	70
Chiapas	A13224	12		011000100000000110101110001101100000000001000001000100001100001000001101010000010						
Chiapas	A13225	13		01100111000100000010101011010100000000100000100						
Chiapas	J4055	11		101001000000001000100110110000000000100010100						
Chiapas	J4056	1		011000100000100						
Chiapas	J4058	15		10010001100001100011110000000010100000100						
Chiapas	J4060	16		0000001010000111011010001101100000000101000010000001000000010000000100000001000000000						
Chiapas	J4061	17		010000101000001110110100011011001000001010000010100001010000010100000010100000101000000						
Colima	A12699	22		0000011001010000100011100010110000000100011000000000100111000001001001001001010000						
Guerrero	J4029	19		0100000000000011000000101100101000000000011000100000000000000000000000000000000000000						
Guerrero	J4066	6		0000101011101000010111101110001100001000001000001000000100000010000001000000101000000						
Guerrero	J4067	2		0000101011100						
Guerrero	J4069	30		00001000010100000011000						
Guerrero	A4510	20		000110000000100						
Guerrero	K82218	23		010001001000001001001010100						
Guerrero	J4107	39		00000000100						
Guanajuato	R32522	52		1011100001010000100001010100000010011001101000000000101000000000000000000000000000000						
Hidalgo	J4109	40		000110000101000011000001010100100000011001101001110000010100000010100000010010000011000						
Hidalgo	J4111	41		0001010001001000000010101000000000110011110001100001010000000000000000000000000000000						
Hidalgo	J4112	42		0001000000001001110101010100100000010011110101000001010000000000000000000000000000000						
Jalisco	A3707	72		0001110000001000100001010010001100001000100010001000000000000000000000000000000000000						
Jalisco	J4076	67		0001100001001000100101100101000000001101000001100000010100000000000000000000000000000						
Jalisco	J4077	44		0001100000101000001000001010100100000000011010000011000000101000000000000000000000000						
Jalisco	J4078	45		000100000101000000100001010100100						
Jalisco	J4079	68		0111010010010000100101100101000110000001101001000010010010000100001000010011100000						
Jalisco	J4080	69		0000101001110000010000010011001000011011000011011100001000001010001000010010011100000						
Jalisco	J4081	70		00011000001010000001001011001001000						
Jalisco	J4082	71		00010000000111000100101001000						
Jalisco	J4083	21		000000010000100						
Mexico	A13275	3		000001010111000000101111000110000010000010000100001011000000111000000111000000110000000						
Mexico	J4020	59		0000000011000100110000010011000000100111000001000000000000000000000000000000000000000						
Mexico	J4021	60		0000000011000100110100001001000						
Mexico	J4023	61		0000000000100						
Mexico	J4025	62		000000001100011011000100100						
Mexico	J4026	63		0000000011000100100100100						
Mexico	K82260	46		00010000001010000100100110100						
Michoacan	A13291	76		0000000011010010010001000						
Michoacan	A13296	48		0000001001000001100000111010101000000010011110010000010100000000000000000000000000000						
Michoacan	A13309	7		01101010101010000101000111100011000001100001000						
Michoacan	J4032	73		0111100001011100001010000101100011000001100001000001100000000000000000000000000000000						
Michoacan	J4036	74		000000001100000000010001100						
Michoacan	J4037	75		0010010011000100100010000100000110000011000010001001001000010010000100100000000000000						
Michoacan	J4074	64		0000000010000010110100100001001000001100001010000110000000000000000000000000000000000						
Michoacan	J4075	47		00010000001000000101000000101001000						

TABLE 2. CONTINUED.

State	Accession	OTU	1	10	20	30	40	50	60	70
Morelos	A12937	8	0000100010101000000101110101110001100000110000010000001000000101110000000							
Morelos	J4009	24	10000010010100000011100000010000000000010010000000000000000000000000000101010							
Morelos	J4015	66	00000001000000000001000010010000000001000000000000000000000000000000000110000							
Nayarit	J4087	31	000010000100000100100							
Nayarit	J4088	9	00100001010100001010000101110001100000110000100000110000000000000000000000000							
Nuevo Leon	J4115	55	00001100000010101000001001010001100000100000100001000010001000011010011001000							
Oaxaca	A13138	29	000010001001010000010001010000000001000							
Oaxaca	J4041	4	10101000100000100011010001101000000000001000000000000000000000000000000000000							
Oaxaca	J4043	57	01101000000101010001101000110000110000010001010001001010001010001010001001000							
Oaxaca	J4048	18	00000100110000000001000000100000000110000010000000000000000000000000000000000							
Oaxaca	J4049	28	00001000100101000001000							
Oaxaca	J4051	14	01100010000000101000100011010000001000100000100000000000000000000000000000000							
Oaxaca	J4052	5	1011100100010101000011001010001100000100000100000011010000110100011000001000							
Oaxaca	A4293	25	0001110001000100100000100101000000000100010100000001100000000100101100000000							
Puebla	J4039	27	00000000100100100010100001000001000							
Puebla	J4040	26	01001000010010000011110011011000000000101010000000100100000000000000000000000							
Sinaloa	J4102	10	0110100000110000001010000010100							
S.L. Potosi	A13316	65	000101001001000							
S.L. Potosi	J4003	56	00000000001000100001100101000110000010000010001000001000000000000000000000000							
S.L. Potosi	J4004	43	00010000000100110100000010100100000001000100000100000000000000000000000000000							
S.L. Potosi	A4056	58	0110100000010101000010010001100011000							
Tamaulipas	J4113	53	0110110000001010100001000101000							
Tamaulipas	J4114	54	00001100000010101000001001000011000							
Zacatecas	A12624	51	00001000010010000000000010101100000000110100100010000010000000000000000000000							
Zacatecas	J4103	37	00000000100							
Zacatecas	J4104	38	00000000100							
Zacatecas	J4105	49	000000000100100000000000101000000000100							
Zacatecas	J4106	50	000000000001000							
Aspicarpa	I526	32	0000101000001010000100000100101101000							
Janusia	A12539	33	0001010000000101010000011001000001000							
Janusia		34	000100011000000010101010000010100000100							
Stigmaphyllon		36	00010010100							

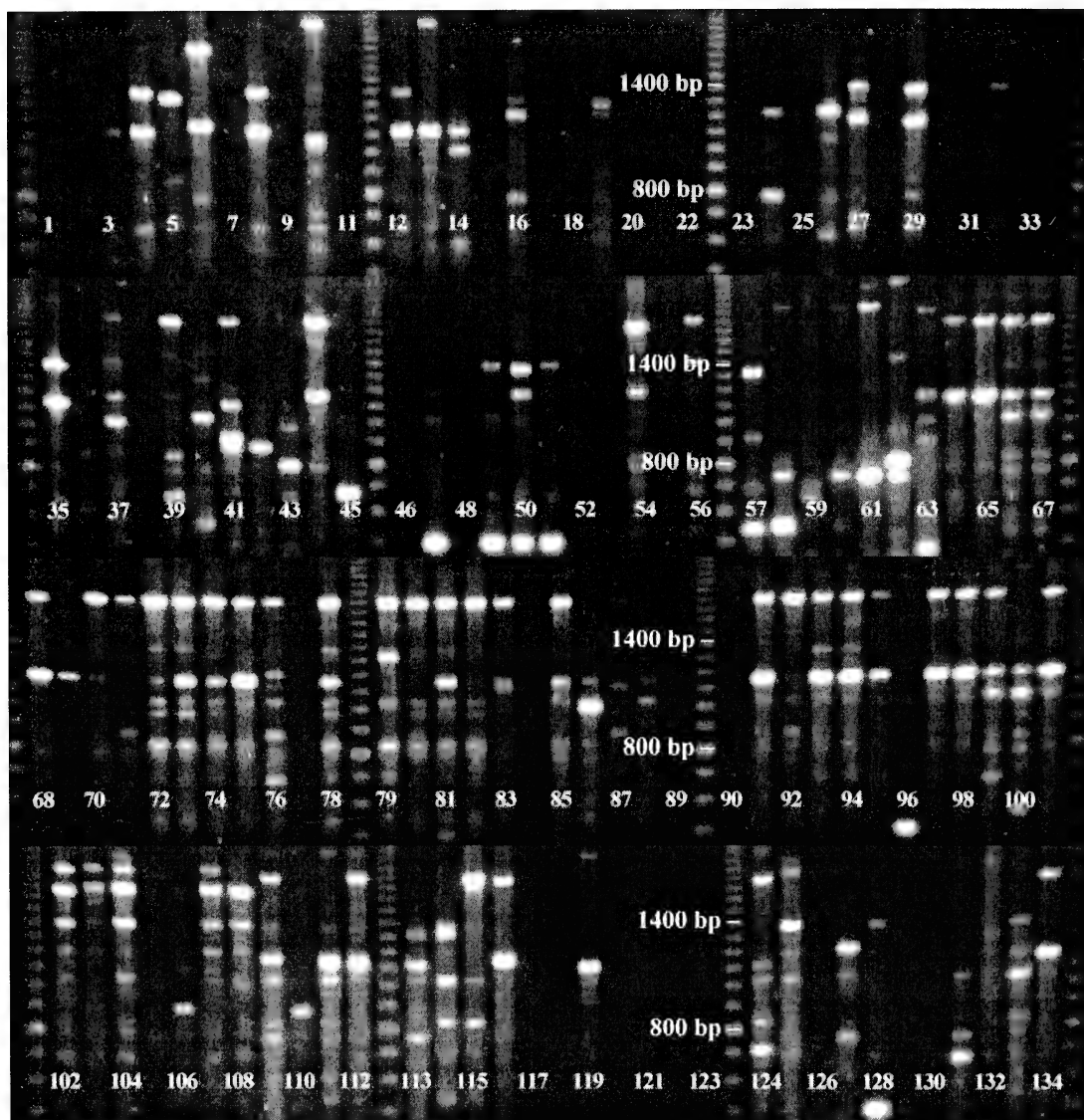


FIG. 1. Example of RAPD products on agarose gel, in this case amplified with primer A-19. Gels were stained with ethidium bromide and visualized with UV transillumination. Molecular weight marker fragments are 100 bp apart. Lane numbers and the 800 and 1400 bp marker fragments are labeled.

plant bearing a section *Zygopterys* cpDNA haplotype (OTU 57) maps on the left side of the tree. That plant is notable in the morphological similarity of its fruit to other plants with intermediate samaras that carry section *Gaudichaudia* cpDNA haplotypes and map to the same region of the RAPD tree (OTU's 52, 68, 75). It also falls close to OTU 58 which has similar fruit shape but bears section *Tritomopterys* cpDNA haplotype L. OTU 57 is a geographically isolated plant carrying a section *Zygopterys* cpDNA haplotype. A plant from the type locality of *G. chasei* W. R. Anderson (OTU 24),

carrying cpDNA *G. chasei* cpDNA haplotype AE, maps close to the cluster of *G. galeottiana* on the RAPD tree (Fig. 4). A plant with intermediate fruit wing morphology (OTU 26), bearing section *Tritomopterys* cpDNA haplotype A, subtends *G. chasei* on the RAPD minimum spanning tree (Fig. 2). The only other plant collected that carries *G. chasei* cpDNA haplotype AE (OTU 63) is *G. andersonii* Jessup which maps with plants in *G. cycloptera* carrying section *Cyclopterys* cpDNA haplotypes (OTU's 21, 61, 62). The narrowly endemic subshrubs, *G. krusei* W. R. Anderson (OTU 30) and *G.*

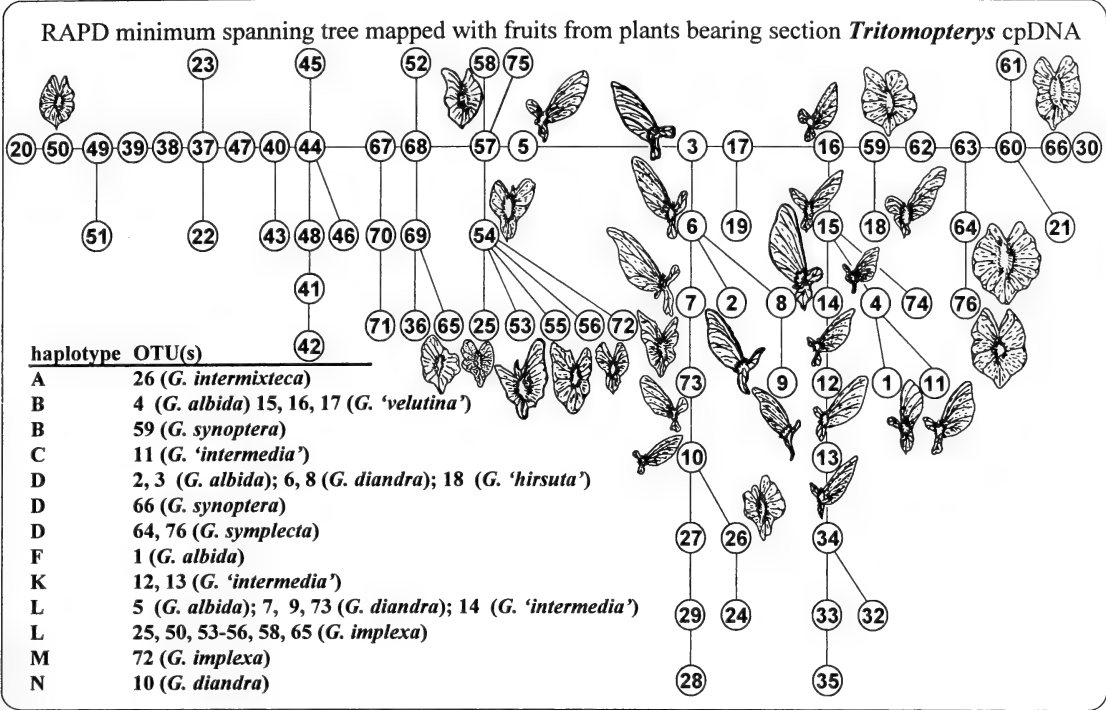


FIG. 2. Samaras from plants carrying cpDNA haplotypes from section *Tritomopterys* plotted on the RAPD minimum spanning tree.

*subverticillata* Rose (OTU 31), map together on the extreme right side of the RAPD tree (Fig. 4). Those taxa are similar in the cpDNA haplotypes they carry as well. *Gaudichaudia subverticillata* and *G. krusei* form the paraphyletic section *Archaeopterys* comprising the internal outgroups to section *Tritomopterys* in the cpDNA haplotype phylogeny (Jesup 2002). OTU 38, which also carries a cpDNA haplotype positioned as an outgroup to section *Tritomopterys* in the phylogeny, has a fruit shape similar to *G. cynanchoides* and maps on the far left of the RAPD tree, close to *G. mcvaughii*.

**Southern hybridization results.** Table 3 presents the results for lanes on the blots that showed hybridization to the probes. The number of fragments per lane hybridizing to the probe is given in the table for each probe used in the study. Chloroplast DNA haplotypes determined with restriction fragment analysis (Jesup 1994, 2002) are also indicated for each lane in Table 3. In each of Figs. 5–10, the probe source is represented by an illustration of a samara at the top of the figure or to one side of the autoradiograph. A line points to the fragment that was labeled for the probe. Superimposed on the image of the autoradiograph are illustrations of samaras from plants that showed strong hybridization to the probe. The results thus presented show

the intersection of data from RAPD's, cpDNA, and fruit wing morphology.

When blots of the RAPD gels were probed with a labeled 1400 bp fragment from lane 12 (Anderson 12937, *G. diandra* (Nied.) Chodat, Morelos, lane 12) all (100%) of the plants expressing the 1400 bp fragment on the gel showed strong hybridization signal (Fig. 5). The surprising result was that all (100%) lanes showing hybridization to the probe hybridized to fragments of different molecular weights as well. Not surprisingly, the 1400 bp fragment (probe source) on the blot showed the strongest hybridization signal. Other fragments showing strong hybridization signal (secondary bands) on the blot showed up on the original gel as faint bands, but none of the secondary bands hybridizing the probes were visible on the gels as bright bands, and some of the secondary bands were not at all visible on the gel. Only rarely (one in twenty) did a lane without a 1400 bp fragment show hybridization to a fragment of a different size (middle frame, bottom panel), and that hybridizing fragment was the same molecular weight as a secondary fragment in lanes with multiple fragments hybridizing to the probe (Fig. 5). The same pattern of results is repeated with the other probes. All bands of the same electrophoretic mobility hybridized to the probe

RAPD minimum spanning tree mapped with fruits from plants bearing section *Gaudichaudia* cpDNA

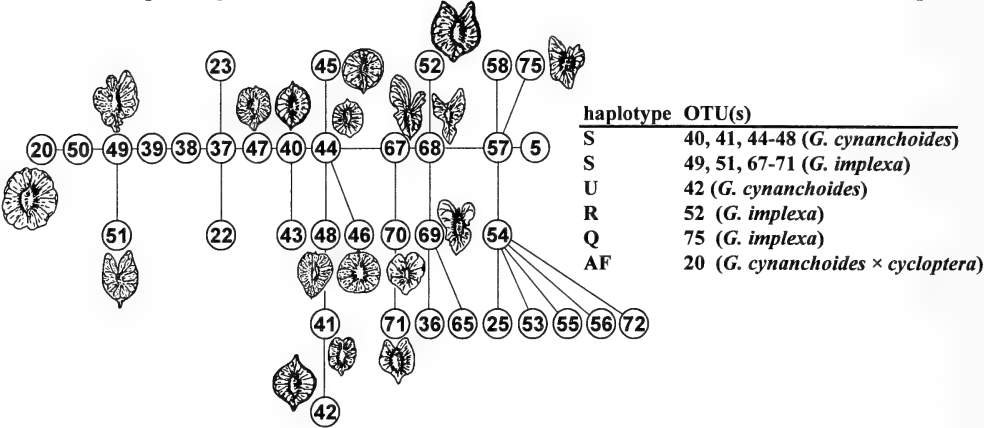


FIG. 3. Samaras from plants carrying cpDNA haplotypes from section *Gaudichaudia*, plotted on RAPD minimum spanning tree. The right side of the tree is omitted since plants carrying section *Gaudichaudia* haplotypes are restricted to the left side of the tree.

made from a band at that location. This clearly demonstrates that bands of the same molecular weight have sequence homology and can therefore be reliably considered identical by descent, at least in *Gaudichaudia*.

The probe source in Fig. 6 is *G. diandra*. All of the plants hybridizing to the 1400 bp probe are found to cluster with the *G. albida* complex (section *Tritomopterys* and intersectional hybrids with section *Tritomopterys*) in the RAPD minimum

RAPD minimum spanning tree mapped with fruits from plants bearing cpDNA haplotypes from sections *Cyclopterys*, *Zygopterys*, *Archaeopterys*, and *Oligopterys*

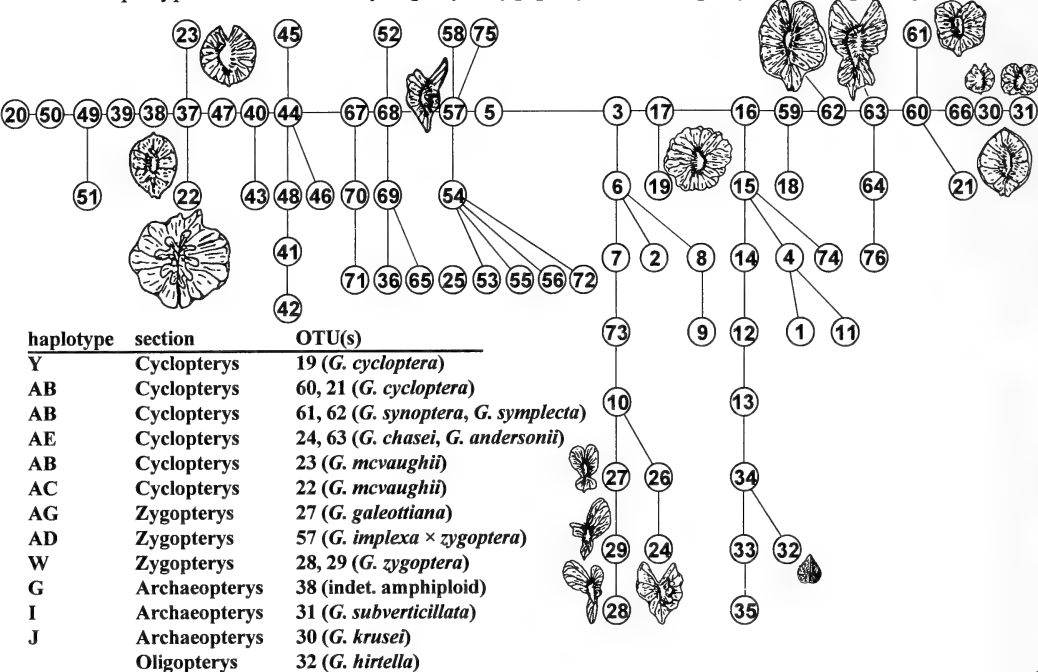


FIG. 4. Samaras from plants carrying cpDNA haplotypes from section *Cyclopterys*, section *Zygopterys*, section *Archaeopterys*, and section *Oligopterys*.

spanning tree (Figs. 2–4). The lanes showing hybridization to the *G. diandra* probe represent plants carrying cpDNA haplotypes from sections *Tritomopterys*, *Cyclopterys*, and *Zygopterys*. All of those plants bearing cpDNA from other than section *Tritomopterys* were identified as amphiploids on the RAPD minimum spanning tree.

In the hybridization shown in Fig. 6, the probe (1150 bp) was taken from a member of the *G. cynanchoides* complex (Jessup 4112, Hidalgo, lane 75). The probe was hybridized against the same set of blots shown in Fig. 5 (i.e., from primer A-19 gels, Fig. 1). Again, all of the lanes showing hybridization signal except one are clustered together on the RAPD minimum spanning tree (Fig. 3), including plants identified as *G. implexa*, hybrids with maternal *G. albida* and paternal (pollen donor) *G. cynanchoides*. One lane, representing a plant with a samara morphology diagnostic of the *G. albida* complex (lane 6, Jessup 4052, Oaxaca), shows strong hybridization with the *G. cynanchoides* probe. That lane represents the same plant found clustering anomalously with the *G. cynanchoides* group on the RAPD minimum spanning tree (Fig. 3, OTU 5). The only other lane represented by a *G. albida* samara (lane 119, Jessup 4032, Michoacan) shows a relatively weak signal, suggesting some involvement with the *G. cynanchoides* group, perhaps via introgression. The two strong signals in the right panel of the top gel (Fig. 6) are bound probe from the first run (cf. Fig. 6) that did not melt from the blotted DNA during stripping of the probe. These “ghost band” appear on other blots as well.

The hybridization run represented in Fig. 7 used the same blots discussed above. The probe for this hybridization experiment (1900 bp) is from the same source as that described for Fig. 6 (Jessup 4112, Hidalgo, lane 75). Here again we see mainly plants from the *G. cynanchoides* group hybridizing to the probe (most of gel panel 3). Again we see the anomalous plant from the *G. albida* complex (lane 6, Jessup 4052, Oaxaca) hybridizing to the probe. A possible *G. cycloptera* × *G. cynanchoides* hybrid also shows up on this autoradiograph (gel panel 2). *Aspicarpa*, the putative sister lineage to *Gaudichaudia*, has recently been shown to nest, at least in part, within *Gaudichaudia* (Davis et al. 2001). The *Aspicarpa* accession used in this study (*G. hirtella* (Rich.) Jessup, formerly in *Aspicarpa*), also hybridized to the 1900 bp probe. Three of the suspected amphiploids (*G. implexa*) hybridizing to the 1900 bp probe (gel panel 4) also hybridized to the 1150 bp probe (Fig. 6, panel 4). Two of the amphiploids (*G. implexa*) hybridize to the 1900 bp probe but not to the 1150 bp probe, and two (also *G. implexa*) hybridize to the 1150 bp probe but not to the 1900 bp probe (Fig. 8).

Likewise, within the *G. cynanchoides* complex (Fig. 7, gel panel 3) some plants hybridize to one probe but not the other, while some hybridize to

both (Fig. 8). Plants that hybridized just to the 1900 bp probe all have morphology typical of *G. cynanchoides*, and all bear the cpDNA haplotype S, which is the most common cpDNA haplotype within section *Gaudichaudia*, the *G. cynanchoides* complex (Fig. 3). Two of the three plants binding the 1150 bp probe also bear cpDNA haplotype S. The other plant bears cpDNA haplotype L, the most common cpDNA haplotype the *G. albida* complex. The samara morphology of that plant is, however, more typical of *G. implexa*, the amphiploids between *G. albida* and *G. cynanchoides* (section *Tritomochaudia*). Most of the plants hybridizing to both probes show the samara morphology typical *G. implexa*. Eight out of fifteen plants binding both probes have cpDNA haplotypes from section *Tritomopterys*, indicating their affinity with the *G. albida* complex, six have cpDNA haplotypes from section *Gaudichaudia*, indicating their affinity with the *G. cynanchoides* complex, and one has a cpDNA haplotype identified as a member of section *Archaeopterys*, an outgroup to section *Tritomopterys*.

Experiments using primer sequence CAGGCC-CTTC (primer A-1) yielded similar results (Fig. 9). Blots were probed with two labeled fragments from the gels used to produce the autoradiographs. The first probe was made with a 1400 bp fragment collected from lane 47 (Jessup 4039, *G. galeottiana*, Puebla). The second probe was made with a 1000 bp fragment collected from lane 16 (Jessup 4055, *G. albida*, Chiapas). The first probe (from *G. galeottiana*) hybridized strongly to five collections from section *Zygopterys*, including the source lane (*G. galeottiana*) three lanes representing *G. zygoptera* and one lane representing *G. intermixteca*. Lanes representing *G. krusei* (section *Archaeopterys*) and *G. hirtella* (section *Oligopterys*, formerly in *Aspicarpa*) were also hybridized by the probe. Hybridization signal from lanes representing *G. krusei* and *G. hirtella* were weak, but stronger than hybridization to lanes representing other elements of *Gaudichaudia*. The second probe (from *G. albida*) hybridized strongly to plants in the *G. albida* complex, and to several of the amphiploids. Two plants were hybridized by both probes. One of those plants (Jessup 4047, Oaxaca) carries a cpDNA haplotype (A) from section *Tritomopterys*, the clade associated with the *G. albida* complex. The other plant (Anderson 12990, Oaxaca) carries a cpDNA haplotype (X) from section *Zygopterys*, the clade associated with the *G. galeottiana* complex. From this we can infer that Anderson 12990, carrying RAPD sites from both *G. albida* and *G. galeottiana* and a cpDNA haplotype from the *G. galeottiana* complex, must be derived from a cross between a plant in the *G. albida* complex, the pollen donor, and a plant in the *G. galeottiana* complex, the maternal parent (Fig. 9). The hybrid, Jessup 4047, must have formed the other way around. The pollen donor was from the *G. galeottiana* com-

TABLE 3. LABELED RAPD PROBES HYBRIDIZED TO BLOTS. Numbers of bands hybridizing probes is recorded for all lanes with a strong hybridization to the probe. Lanes that were blank on the gels have been omitted. Collections are grouped by taxonomic assignment based on morphology. Asterisks indicate probe sources.

			Primer Probe								
Collection #	cpDNA	Lane #	A1 16:1000	A1 47:1400	A-2 8:1250	A-3 28:950	A-7 4:850	A-19 12:14000	A19 12:1100	A-19 75:1150	A-19 75:1900
Section <i>Tritomoptety</i> s											
Chi4056	cpDNA 1-F	1			4	2					
Gro4067	cpDNA 1-D	3	2		4	2		4	3		
Mex13275	cpDNA 1-D	4	3		4		*2	4	3		
Oax4041	cpDNA 1-B	5	3		4	2					
Oax4052	cpDNA 1-L	6	3			2			2	2	3
Gro4066	cpDNA 1-D	8	3		*4	2		4	3		
Mic13309	cpDNA 1-L	10	3			2					
Mor12937	cpDNA 1-D	12			4			*4	*3		
Nay4088	cpDNA 1-L	13			4	2			3		
Sin4102	cpDNA 1-N	14	3		4	2			3		
Chi4055	cpDNA 1-C	16	*3		4	2	2				
Chi13244	cpDNA 1-K	18	1		4	2					
Chi13225	cpDNA 1-K	19	3		4	2	2				
Jal4084	cpDNA 1-L	21				2					
Jal4085	cpDNA 1-L	22				2					
Oax4051	cpDNA 1-L	24	3		4	2					
Oax13216	cpDNA 1-K	26	3		4	2	2				
Chi4058	cpDNA 1-B	27				2		4			
Chi4060	cpDNA 1-B	28		4	*2						
Chi4061	cpDNA 1-B	29		4	2	2	4				
Oax4054	cpDNA 1-K	30		4	2						
Oax4048	cpDNA 1-D	32		4			4				
Natural and Artificial Hybrids											
Zac4106	cpDNA 1-L	84		4							
Zac12624	cpDNA 2-S	85		4	2			3	3	4	
Gua4006	cpDNA 1-L	86			4	2				3	
Gua4108	cpDNA 1-L	87									3
Hid32522	cpDNA 1-L	88			4	2	2			3	
Tam4001	cpDNA 1-L	91			4	2			1	3	4
Tam4113	cpDNA 1-L	92			4	2					3
Tam4114	cpDNA 1-L	93			4	2			1		4
Nue4115	cpDNA 1-L	94			4	2			1	3	4
SLP4002	cpDNA 1-L	95							1	3	4
SLP4043	cpDNA 4-AD	97	1		4	2			1	3	4
SLP4056	cpDNA 1-L	98			4	2			1	3	4
Mex4020	cpDNA-1B	102			4	2		3			
Mex4021	cpDNA 1-AB	103			4			3			
Mex4023	cpDNA 1-AB	104			4	2		4			
Mex4025	cpDNA 1-AB	106			4						
Mex4026	cpDNA 5-AE	107			4			3			
Mic4074	cpDNA 1-D	108			4	2		3			
SLP13316	cpDNA 1-L	109			4		2		1	3	2
Jal4076	cpDNA 2-S	111			4				3	3	
Jal4079	cpDNA 2-S	112			4		2		3	3	4
Jal4080	cpDNA 2-S	113				2	2		3		
Jal4081	cpDNA 2-S	114					2				
Jal4082	cpDNA 2-S	115					2				3
Jal3707	cpDNA 1-M	116				2			1	3	4
Mic4031	cpDNA 1-L	118	3								
Mic4032	cpDNA 1-L	119			4				3		
Mic4034	cpDNA 1-L	121				2	2	1			
Mic4035	cpDNA 2-P	122					2				
Mic4037	cpDNA 2-Q	124	3		4	2					3
Mic13291	cpDNA 1-D	125			4	2		2			
Oax4043	cpDNA 4-AD	127	3		4	2					
Oax4044	cpDNA 4-V	128	3	4	4	2		3			



TABLE 3. CONTINUED.

Collection #	cpDNA	Lane #	Primer Probe								
			A1 16:1000	A1 47:1400	A-2 8:1250	A-3 28:950	A-7 4:850	A-19 12:14000	A19 12:1100	A-19 75:1150	A-19 75:1900
Oax4046	cpDNA 1-A	130					2				
Oax4047	cpDNA 1-A	131		2	4	2					
Oax13031	cpDNA 1-A	132			4	2					
H687	cpDNA 1-D	35			4		2	4		3	
H2187	cpDNA 1-L	36			4	2					
H2487	cpDNA 1-M	64			4			3	3	3	4
H5487	cpDNA 1-L	65			4	2	2		1	3	4
H289	cpDNA 1-L	66			4				1	3	4
H489	cpDNA 1-L	67			4				1	3	4
H4387	cpDNA 1-L	99			4		2		1	3	4
H689	cpDNA 1-L	100			4				1	3	
H4687	cpDNA 1-L	101			4	2			1	3	4
H2586	cpDNA 1-L	133	3		4			3		3	
H2687	cpDNA 1-M	134	3			2				3	4
Section <i>Guadichaudia</i> cpDNA											
Zac4103	cpDNA IO-G	68							1	3	4
Zac4104	cpDNA 2-R	69							1	3	
Gua4107	cpDNA 2-R	70							1	3	3
Gua4007	cpDNA 2-R	71									3
Hid4109	cpDNA 2-S	72			4				1	3	4
Hid4110	cpDNA 2-S	73			4				1	3	3
Hid4111	cpDNA 2-S	74			4	2			1	3	3
Hid4112	cpDNA 2-U	75			4				1	*3	*4
SLP4004	cpDNA 2-S	76			4						3
Jal4077	cpDNA 2-S	78					2		1	3	4
Jal4078	cpDNA 2-S	79									3
Mex82260	cpDNA 2-S	80					2				3
Mic4075	cpDNA 2-S	81					2		1	3	4
Mic13296	cpDNA 2-S	82					2				3
Zac4105	cpDNA 2-S	83			4	2			3	3	3
Sections <i>Cyclopterys</i> , <i>Zygopterys</i> , <i>Oligopterys</i> and outgroups											
Gro4510	cpDNA 3-AF	39			4	2	2				3
Jal4083	cpDNA 3-AB	40			4						
Col12699	cpDNA 3-AC	41			4						
Oax4293	cpDNA 1-L	44	3		4	2			1	3	4
Pue4040	cpDNA 1-A	45			4	2					
Pue4039	cpDNA 4-AG	47		*4							
Oax4049	cpDNA 4-W	49		2	4	2		3			
Oax12990	cpDNA 4-X	50	3	4	4		2				
Oax13138	cpDNA 4-W	51			4		2	3			
Gro4069	cpDNA IO-J	54		2							
Asp525	cpDNA ASP	56		2							3
Asp526	cpDNA ASP	57		2							
Jan1254	cpDNA JAN	59					2				
Jan3373	cpDNA JAN	61					2				

plex and the maternal lineage from the *G. albida* complex (Fig. 9).

Blots made from gels of RAPD produced with primer sequence TGCCGAGCTG (A-2) were probed with a labeled 1250 bp fragment from *G. diandra* (lane 8, Jessup 4066, Guerrero) (Table 3). The probe bound strongly to RAPD fragments from plants throughout the genus. About 77% of the plants sampled in the *G. albida* complex hybridized the probe, but only 40% of the plants sampled in the *G. cynanchoides* complex hybridized the probe. About 76% of the plants sampled from among the

amphiploids hybridized the probe. Representatives from *G. cycloptera*, *G. mcvaughii*, and *G. galeotiana* also bound the probe.

Blots made from gels of RAPD fragments produced with primer sequence AGTCAGCCAC (A-3) were probed with a labeled 950 bp fragment amplified from an unpublished species in the *G. albida* complex (lane 28, Jessup 4060, Chiapas) (Table 3). About 86% of the plants sampled in the *G. albida* complex hybridized the probe. Only 13% of the plants sampled in the *G. cynanchoides* complex hybridized the probe. About 53% of plants sampled



RAPD A-19: Primer sequence: 5'CAAACGTCGG3'

Probe source: lane 75, ~1150bp; Hidalgo

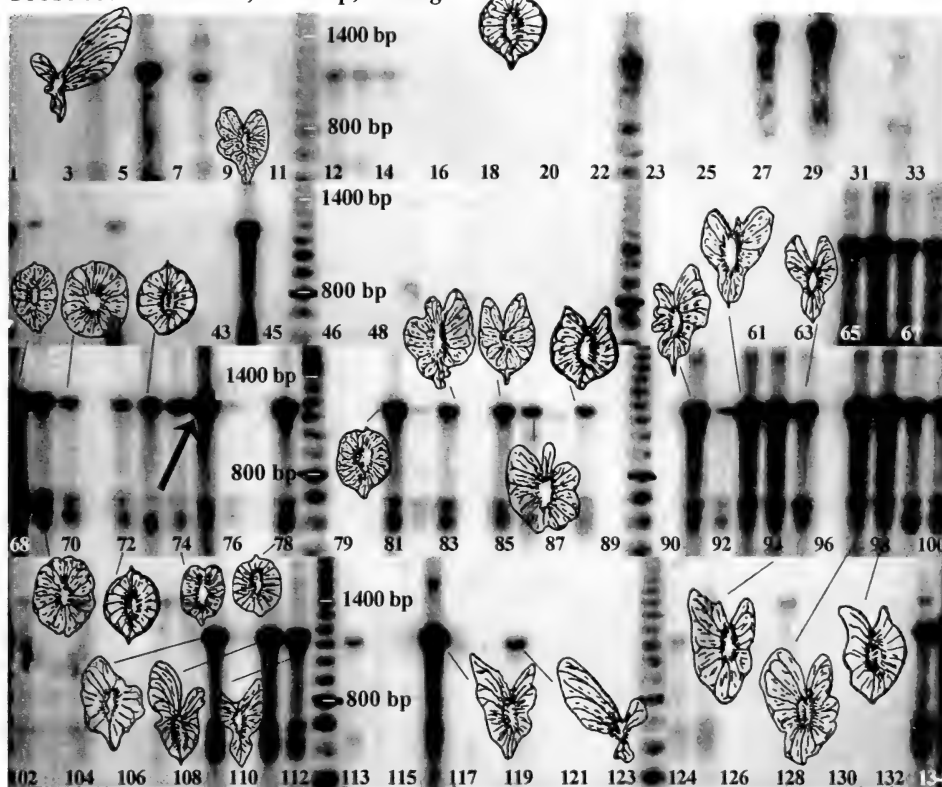


FIG. 6. Autoradiographs of RAPD products from primer A-19 (blotted from gels in Fig. 1) probed with 1150 bp fragment from lane 75 (Jessup 4112, *G. cynanchoides*, Hidalgo), indicated by arrow. Fruits are illustrated in lanes showing strong hybridization to the probe for all plants with fruits available.

would be to sequence several sites having the same molecular weight, but that approach is expensive and would be limited to relatively few specimens. Use of RAPD hybridization blots permits screening a large set of DNA's, in this study representing 75 plants in the genus. The procedure probes a radio-labeled RAPD fragment of known size and source against Southern blots made from the RAPD gels. RAPD fragments on the blot hybridizing to the labeled probe must have substantial sequence homology for strong hybridization. In the experiments reported here only lanes that showed a strong hybridization signal were included in the data matrix. Many lanes showed weak binding of the probe and might have some sequence homology, but divergence was sufficient to weaken the signal. Weak hybridization is expected from the primer sequence alone.

*The assumption of independence.* In addition to the question of sequence homology of RAPD fragments of the same weight across samples, there is the question of sequence homology of RAPD fragments of different weight within a sample. Since

both the theory of how RAPD markers behave in amphiploids and the empirical evidence presented here suggests that hybrids combine distinct RAPD sites of the parental lineages, we expect that some of those sites will be homologous, or more specifically, synologous (Mindell and Meyer 2001)—divergent and descended from a common ancestor but residing in the same genome by virtue of reticulate ancestry. Synologous fragments would have sufficient sequence divergence (insertions, deletions, substitutions) to express different electrophoretic mobility, but would retain enough sequence homology to hybridize to a probe from the synologous locus. Changes in size of a RAPD site caused by insertion/deletion events are likely to develop in reproductively isolated lineages. When the lineages bearing the divergent sites merge in an amphiploid each will be expressed, resulting in complementation. In the absence of recombination between parental genomes the hybrid lineage would then be a fixed heterozygote. Detection of fixed heterozygosity corroborates other evidence supporting an amphiploid origin of the lineage. It is tempting to in-

**RAPD A-19: Primer sequence: 5'CAAACGTCGG'**  
**Probe source: lane 75, ~1900bp; Hidalgo**

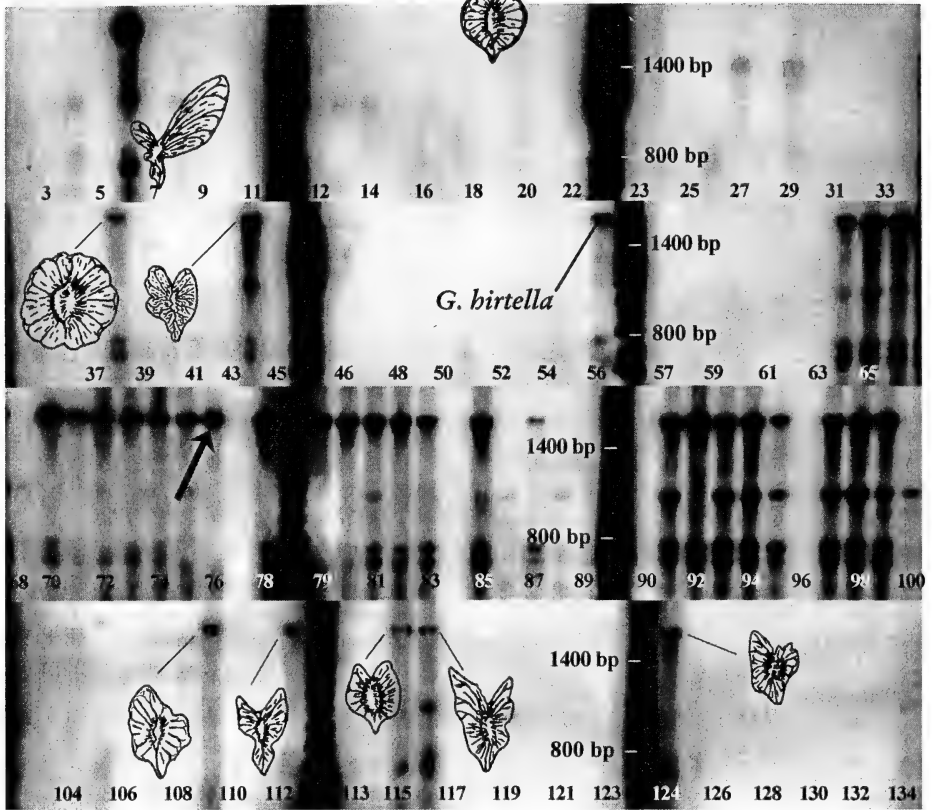


FIG. 7. Autoradiographs of RAPD products from primer A-19 (blotted from gels in Fig. 1) probed with 1900 bp fragment from lane 75 (Jessup 4112, *G. cynanchoides*, Hidalgo), indicated by arrow. Fruits are illustrated in lanes showing strong hybridization to the probe for all plants with fruits available.

terpret multiple bands with sequence homology as indicating successive layers of fixed heterozygosity built up in the tiered genomes of an ancient polyploid complex.

The evidence presented here is consistent with synologous origins for fragments that bind the probe but which have different molecular weights from that of the probe. Competing hypotheses can not, however, be ruled out with the available data. For example, multiple fragments hybridizing the probe within a specimen could indicate multiple nested priming sites within the amplification window of PCR conditions used. Some PCR products would encompass three pairs of priming sites, some two, and some only one, resulting in three fragments sharing overlapping sequence identity. Other scenarios explaining the appearance of different sized RAPD fragments with sequence homology can be envisioned. Without a detailed study of how the coamplifying fragments are arranged on the chromosomes it is not possible to support or reject the alternative hypotheses.

*Introgression.* A plausible explanation for the observation that all plants binding both the A-19 1900 bp and A-19 1150 bp probes show morphology typical of hybrids between *G. cynanchoides* and *G. albida* (Fig. 8) is that cryptic sibling species within *G. cynanchoides* are forming tetraploids and crossing, and those polyploids are capable of forming amphiploids with similar lineages from the *G. albida* complex. It is quite possible that some lineages in the *G. cynanchoides* complex (and in other groups as well) are geographically restricted whereas the polyploid lineages involved in most of the wide crosses are weedy and wide ranging and carry more of the genetic diversity as fixed heterozygosity.

If we compare the autoradiograph of the A-19 1150 bp probe (Jessup 4112, *G. cynanchoides*, Hidalgo, lane 75), and that of the A-19 1100 bp probe (Anderson 12937, *G. diandra*, Morelos, lane 12) for just eight plants from the *G. cynanchoides* complex (lanes 81–88) (Fig. 10), we observe one plant hybridizing only to the 1100 bp probe (probe from

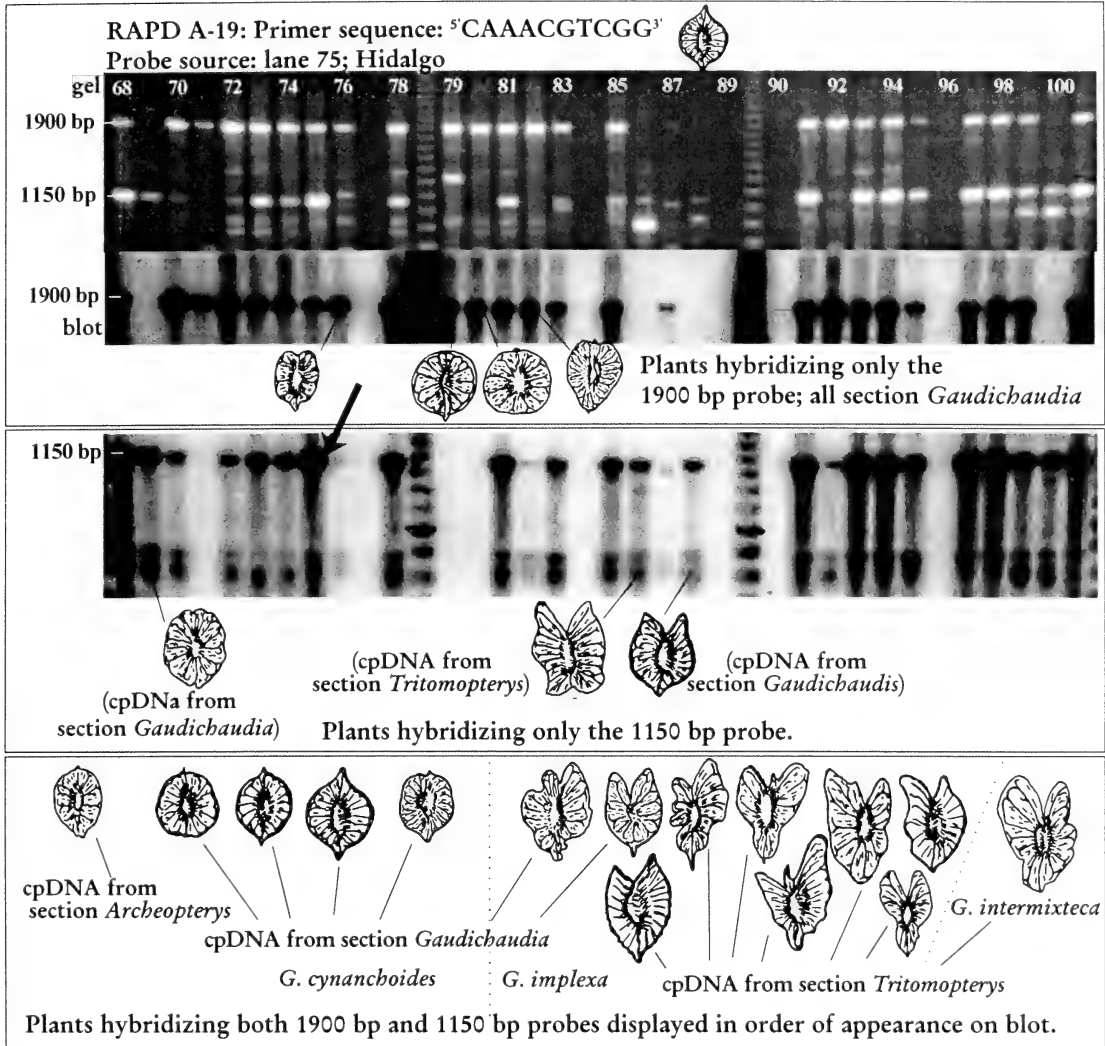


FIG. 8. Autoradiographs of RAPD products from primer A-19 (blotted from gels in Fig. 1), lanes 68–101. Gel, at top, is compared with autoradiographs from 1900 bp probe and 1150 bp probe. Both probes were prepared from fragments in lane 75 (Jessup 4112, *G. cynanchoides*, Hidalgo), indicated by arrow. Fruits illustrated top panel are from plants hybridizing only the 1900 bp probe; fruits illustrated middle panel are from plants hybridizing only the 1150 bp probe; fruits illustrated bottom panel are from plants hybridizing both the 1900 bp and 1150 bp probes. In bottom panel sectional affiliation of cpDNA haplotypes is indicated for each fruit illustrated, and dotted lines separate described species.

*G. albida* sens. lat.), two plants hybridizing only to the 1150 bp probe (probe from *G. cynanchoides*), and three plants hybridizing to both probes. The plants hybridizing both probes all carry cpDNA haplotypes characteristic of section *Gaudichaudia*. Two of the three plants hybridizing both probes are *G. implexa* (nothosection *Tritomochaudia*) and exhibit the samara morphology of the amphiploids. The plant hybridizing only the 1100 bp probe carries a cpDNA haplotype from section *Tritomopterys*, the *G. albida* complex. Of the two plants hybridizing only the 1150 bp probe, one carries a

cpDNA haplotype from section *Tritomopterys*, and one carries a section *Gaudichaudia* cpDNA haplotype.

One explanation for sites shared in this way is that introgression is occurring between the *G. diandra* lineages and the *G. cynanchoides* lineages. The 1100 bp probe (from *G. diandra*) hybridizes to several plants in the *G. albida* group, and to almost every plant in the *G. cynanchoides* group. Among the plants in the *G. cynanchoides* group, plants that exhibit the typical cynanchoid samaras hybridize only a single fragment, the 1100 bp fragment. In



gle RAPD site. Hybrids exhibit complementation of sites from parental lineages that are presumably fixed for different size fragments. This allows us to use the presence of fragments on the gels as binary characters in phenetic analysis of relatedness among the collections, even though different size fragments have homologous sequences.

We can get even more specific in identifying the parental lineages for a given hybrid by combining information from the Southern transfer hybridization experiment with information from analysis of cpDNA restriction site data. The experiments using primer sequence CAGGCCCTTC (primer A-1) demonstrate this application of RAPD hybridization (Fig. 9). From the forgoing evidence it seems likely that RAPD fragments of different molecular weights but similar sequence, as demonstrated by strength of probe hybridization, can be used to characterize genomes within polyploids. Markers thus developed can be used to resolve reticulate ancestry in amphiploid complexes that are otherwise intractable.

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LONG-TERM POPULATION DYNAMICS OF NATIVE *NASSELLA*  
(POACEAE) BUNCHGRASSES IN CENTRAL CALIFORNIA

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ABSTRACT

California bunchgrass communities are one of the most endangered ecosystem types in the United States. In this study, we sought to determine long-term (52+ years) changes in populations of native bunchgrasses, *Nassella pulchra* (A. Hitchc.) Barkworth and *Nassella cernua* (Stebb. & Love) Barkworth, in unmanaged stands. At the landscape scale, *Nassella* has increased. However, population dynamics of individual stands appeared related to land-use history. Non-native annuals, by themselves, did not seem to cause decline of *Nassella* stands, but light grazing did cause reduction of *Nassella* basal cover. Areas that were historically cultivated supported *Nassella* stands with lower basal cover and size distributions qualitatively different from areas that were never cultivated. Mortality of *Nassella* was concentrated in small plants. Interspecific interference probably was important in limiting seedling recruitment in stands with low *Nassella* basal cover, and intraspecific interference appeared to become important as *Nassella* basal cover increased. Even in the presence of non-native annuals, *Nassella* stands in areas that have not been disturbed by cultivation do not appear to require management for maintenance. New individuals are recruiting into populations, and conservative estimate of longevity of large individuals of *Nassella* is 100 years. However, in areas that have been cultivated, active management may be required to increase the abundance of *Nassella*.

Key Words: California, *Nassella*, grassland, survival, longevity, long-term.

INTRODUCTION

Perennial bunchgrass communities are one of the rarest plant communities in California (Keeley 1989, 1993) and are considered to be one of the most endangered ecosystem types in the United States (Noss et al. 1995; Peters and Noss 1995). Since the founding of the Spanish missions in the mid-1700's, massive invasions of annual grasses from the Mediterranean basin have altered native communities to such a degree that today the original extent and composition of these communities is unknown (Keeley 1989; Heady et al. 1992; Hamilton 1998). Today in California, an area of approximately 7,000,000 ha is dominated by non-native annual grasses (Huenneke 1989). In many cases, these non-natives comprise from 80% to 100% of the cover (Biswell 1956; Heady 1956; Macdonald et al. 1988; Heady et al. 1992), and the small patches of perennial bunchgrasses that still exist in California (including *Nassella* (= *Stipa*) *pulchra* (A. Hitchc.) Barkworth and closely related *Nassella cernua* (Stebb. & Love) Barkworth) always include non-native grasses.

In most of California, the original community composition of areas in which *Nassella* bunchgrasses are found today is a matter of conjecture (Hamilton 1998). However, it is clear that over the past two hundred years, the biotic environment has changed dramatically for these bunchgrasses (Dyer and Rice 1999). There are no 'pristine' areas of California grassland left. Non-native annual grasses such as *Bromus hordeaceus* L., *Bromus diandrus* Roth, *Avena fatua* L., and *Avena barbata* Link have invaded every known bunchgrass stand. Furthermore, due to land clearing, farming, and extreme over-grazing (Burcham 1957), even areas that are currently protected have been previously disturbed in some manner. Because of a lack of long-term studies, it is unknown whether a new steady-state situation has been achieved in the California grasslands, or whether bunchgrass stands are still adjusting to the altered conditions.

In California, there is a growing interest in restoration and conservation of *Nassella* bunchgrass communities (Knapp and Rice 1994; Stromberg and Kephart 1996; Carlsen et al. 2000; Kephart 2001). Attempts at generalized management prescriptions that promote grazing and/or burning as a tool to reduce competition from annual grasses and enhance longevity of mature bunchgrasses have been proposed (e.g., Menke 1992) for inland sites. Substantial differences are evident between inland

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and coastal native grasslands where *Nassella* is a co-dominant (Stromberg et al. 2001). On inland sites, recruitment of *Nassella* appears to be limited by competition by non-native annuals (Dyer and Rice 1999) and management strategies have been developed to improve establishment by reducing exotic seed banks (Stromberg et al. 2002). Studies of mortality and recruitment, along with restoration, are lacking in coastal environments of California and management strategies suggested or inland sites (Menke 1992) may require modification. We lack the fundamental information concerning long-term stability characteristics of *Nassella* stands in the face of competition from non-native annual grasses. Because of this, land managers have been forced to rely on hearsay to determine whether native grasslands require management in order to persist, and if so, what kind. Results from short-term studies (one-two years) have tended to be unreliable indicators of longer-term dynamics. For example, in one study, preliminary results after 16 months indicated that burning and early-spring grazing were effective at increasing *Nassella pulchra* seedling establishment and survival (Fossum 1990). However, in the same study, after four years, it was concluded that burning and grazing were not effective at enhancing *Nassella pulchra* seedling recruitment (Dyer et al. 1996).

In our study, we sought to determine long-term changes in populations of *Nassella* bunchgrasses in unmanaged stands. In particular, we asked: (1) In the absence of fire or grazing, has *Nassella* increased or decreased at the landscape scale? (2) At the scale of individual stands, are established populations of *Nassella* stable? (3) At the scale of single individuals, is there life-stage-related mortality that suggests interference from non-native grasses? (4) Do trends in multi-scale population dynamics suggest that *Nassella* requires management for persistence when there is interference from non-native annuals?

There are very few sites in California where data exist that allow for analysis of long-term trends in *Nassella* bunchgrass populations. One such place is the Hastings Natural History Reservation in the foothills of the South Coast Range in central California. Here, in a study initiated in 1944 by G. L. Stebbins, White (1966) described old field succession over a 22-year period. Using unpublished data from studies by both Stebbins and White and more detailed data from a number of other bunchgrass stands at Hastings Reservation, we have been able to extend the original findings of White to encompass a period of 52 years, and to compare a number of sites around Hastings Reservation representing many ecologically distinct situations with different land-use histories.

#### METHODS

The 911-ha Hastings Natural History Reservation (36°33'30"N, 121°33'30"W) is located in the

interior foothills of the coastal Santa Lucia Mountains in central California, 33 km southeast of Monterey. The Mediterranean climate, characterized by hot, dry summers and cool wet winters, supports a number of plant communities including oak woodland, chaparral, and grassland (Griffin 1971; MacRoberts and MacRoberts 1976; Williams and Koenig 1980). Hastings Reservation has been protected from fire and grazing since its establishment in the fall of 1937, except for a 40 ha horse pasture that was lightly grazed until 1968.

Between 1944 and 1977, several plots were established at sites with a variety of land use histories (all within four km of each other) around Hastings Reservation to monitor native *Nassella* (including both *N. pulchra* and *N. cernua*) bunchgrasses (Table 1; detailed maps showing stand locations are available at Hastings). Original plots were established to monitor small patches of *Nassella* that remained, for whatever reason, in what was often a much larger expanse of introduced, annual grasses on abandoned fields or in oak savanna. Because data collection for these plots was not coordinated, available data differed for each plot. Data collected ranged from multiple censuses of size and location of every *Nassella* individual in a given plot, to single censuses indicating only presence or absence in a plot. The two species of *Nassella* that occur at Hastings Reservation are extremely similar in vegetative morphology and are known to hybridize (Stebbins and Love 1941; Love 1954). Because many of the data sets for plots did not differentiate between these closely related species, we did not differentiate these species in our data analysis. All nomenclature follows Hickman (1993).

We used data from nine plots (Table 1) that were established in four areas at Hastings Reservation: White Prairie (one plot), South Sandstone (one plot), North Field (five plots), and Arnold Field (two plots). White Prairie, South Sandstone, and North Field are all within a few hundred meters of each other (elevation ca. 550 m), and Arnold Field (elevation ca. 730 m) is located approximately four km SW of the other three areas. *Nassella* bunchgrasses (also known as tussock grasses or tufted grasses) are perennial grasses that have a clumped or caespitose growth habit. For all plots, *Nassella* individuals were defined as any physically distinct tussock that was not clearly a clonal fragment from some larger tussock (see e.g., Wilhalm 1995).

An analysis of size structure of the *Nassella* populations was based on historical data or 1996 measurements of basal diameter measurements of individuals. For many plots, historical data were taken from detailed tracings or maps of individual plants. Plants were divided into size classes based on basal diameters: (1) less than or equal to one cm, (2) greater than one cm to 5 cm, (3) greater than five cm to 10 cm, and (4) greater than 10 cm. Plants that were not circular were assigned to diameter classes based on the corresponding basal ar-

TABLE 1. SUMMARY INFORMATION FOR PLOTS USED IN THIS STUDY.

Plot name	Plot area (m <sup>2</sup> )	Date established	Notes
White Prairie	10	1977	Considered to be undisturbed relict of bunchgrass prairie; moderate gopher activity
South Sandstone	10	1966	Never cultivated; in a 40 ha area lightly grazed by 2–5 horses 1940–1968
North Field 427	149	1966	Originally woodland; lightly cultivated for barley ca. 1860–1937
North Field 428	56	1966	Originally woodland; lightly cultivated for barley ca. 1860–1937
North Field 429	84	1966	Originally blue oak woodland; lightly cultivated for barley ca. 1860–1937
North Field 409	9	1965	Sub-plot of North Field 429
North Field 412	9	1964	Originally valley oak savanna; cleared; cultivated as vineyard ca. 1920–1937
Arnold 420	9	1964	Originally valley oak savanna; cleared; cultivated barley ca. 1860–1937; many gophers
Arnold 449	10	1979	Probably lightly cultivated 1860–1937; burned in 1979, many gophers

eas. To estimate minimum longevity of *Nassella* individuals, we used direct tagging of plants. We estimated the age of large individuals by determining average rates of increase in basal area and calculating the number of years required for an individual to attain a given size.

The plot in White Prairie was established in 1977. This plot is surrounded by oak woodland and, as there is no record of land clearing, the original vegetation was probably grassland. White Prairie is considered to be a relict of pre-European *Nassella* bunchgrass grassland because it has not been cleared, and was probably only occasionally grazed. The plot showed evidence of moderate gopher (*Thomomys bottae*) activity. In 1977, individual *Nassella* plants were tagged, and, in many cases, wire loops were placed around the base of the plants to ensure future identification of individuals. Historical data include scale maps showing location and shape of each *Nassella* individual, as well as basal diameter measurements. In most cases *Nassella* individuals were generally elliptical or circular, and, because of the detail of the maps, it was possible to identify individuals that were more irregular in shape. A digital image analysis system (Decagon Devices, Pullman Washington) was used to calculate basal area of irregular-shaped clumps. In the 1993 census, many tags could not be re-located; however, carefully drawn maps from 1977 allowed us to identify most individuals.

The plot in South Sandstone was established in 1976. This plot is located adjacent to oak woodland, and, like White Prairie, the original vegetation was probably grassland. The South Sandstone plot was never cleared or cultivated, but is located in a 40-ha pasture that was lightly grazed by two to five horses until 1968. In 1976, individual *Nassella* plants were tagged using the same methods as previously described. Historical data include scale

maps showing location and shape of each *Nassella* individual, as well as basal diameter measurements. Almost all original tags in the South Sandstone plot were re-located in the 1993 census and, thus, temporal comparisons are always on the same individuals. A separate study using the South Sandstone plot counted *Nassella* seedlings in 1976, 1977, 1978, and 1979.

The five plots in North Field were established between 1964 and 1966 (Table 1), and are all located within about 60 m of each other. Before 1900, North Field was probably oak woodland dominated by *Quercus douglasii* (White 1966). Around 1900 the trees were cleared, and the relatively level plots 427, 428, and 429 (including 409, a subplot of 429) were cultivated for barley. Plots were located on clay-sand soils with rock outcrops. Although the field was cultivated for small grain production, only mule-drawn implements were used. Isolated, rocky outcrops where *Nassella* persisted were relatively undisturbed by the light cultivation equipment used during farming. North Field plot 412 occurs on a slope and was a vineyard. Data for North Field plots 427, 428, 429, and 409 from 1966 (1964 for plot 409) were taken from maps on which number and approximate location (but not size) of *Nassella* individuals were recorded. In the 1996 re-census, in order to calculate basal cover, two orthogonal diameters were recorded for every individual and basal area calculated (assuming an ellipse). *Nassella* individuals in North Field plot 412 were mapped over a period from 1964 through 1996. In 1977, 1993, and 1996, basal area of each individual was also measured. All five North Field plots are included in a larger area that had been monitored since 1944. Available data from 1944 through 1964 indicate only whether or not *Nassella* bunchgrasses were present in the larger area.

The two plots in Arnold Field were established

TABLE 2. TOTAL BASAL AREA OF *NASSELLA* IN PLOTS AT HASTINGS RESERVATION (cm<sup>2</sup>/m<sup>2</sup>).

Year	White Prairie	South Sandstone	North Field 412	North Field 427	North Field 428	North Field 429	Arnold 420
1964	●	●	●	●	●	●	400
1976	●	740	●	●	●	●	●
1977	1140	770	370	●	●	●	●
1993	1190	1180	0	●	●	●	●
1996	●	●	19	250	310	290	670

in 1964 and 1979 (Table 1). Before 1937, these two plots were probably dominated by chaparral, since they occur near stands of *Adenostoma fasciculatum* Hook. & Arn., and 20% of Arnold 449 was covered with this shrub in the 1996 re-census. Plots in Arnold field area also on relatively shallow soils with rocks near the surface, and may not have been deeply tilled with the mule-drawn discs used at the time. Both Arnold plots show evidence of very high gopher activity. Historical data include scale drawings of *Nassella* individuals in Arnold 420 (used to obtain information on density and basal diameter of *Nassella* in 1964) and rough drawings for Arnold 449 (used to calculate density). In the 1996 re-census, basal areas were calculated as for the other areas.

RESULTS

Basal area of *Nassella* showed different patterns of change in different plots (Table 2). The relict White Prairie plot was essentially constant over the 16-year period from 1977 to 1993. *Nassella* at South Sandstone increased in basal area over this

time period, achieving in 1993 a value essentially the same as White Prairie. There were insufficient data to draw conclusions about changes in total basal cover of *Nassella* in North Field, except for plot 412 (former vineyard). In this case, *Nassella* disappeared between 1977 and 1993; however, in 1996, a very small amount of *Nassella* was again found in this plot. In Arnold 420, *Nassella* basal area increased between 1964 and 1996.

Density of *Nassella* individuals also showed different patterns of change in different plots (Table 3). The relict White Prairie plot had the highest density of all measured plots in 1977 and exhibited a slight increase with time. Mature *Nassella* individuals at South Sandstone decreased by about 50% between 1976 and 1993, even though *Nassella* seedling recruitment pulses temporarily increased total *Nassella* density in 1978 and 1979. In North Field 412 (former vineyard), density of *Nassella* increased from 1951 until 1970, and then declined to zero by 1993. In 1996, three individuals were again found in this plot. In North Field plots 427 and 428, *Nassella* density increased between 1966

TABLE 3. DENSITY OF *NASSELLA* (PLANTS/m<sup>2</sup>) FOR PLOTS AT HASTINGS RESERVATION. Missing entries indicate that plots were not yet established or were not measured in that year. <sup>a</sup> Density of mature individuals only is 12.2. <sup>b</sup> Density of mature individuals only is 11.7.

Year	White Prairie	South Sand- stone	North Field 412	North Field 427	North Field 428	North Field 429	North Field 409	Arnold 420	Arnold 449
1944	●	●	none	none	none	present	present	●	●
1945	●	●	none	none	none	increase	present	●	●
1946	●	●	none	none	none	increase	present	●	●
1947	●	●	none	none	none	stable	present	●	●
1951	●	●	present	present	none	increase	present	●	●
1964	●	●	1.8	present	present	increase	2.8	3.3	●
1965	●	●	1.9	●	●	●	2.9	●	●
1966	●	●	●	0.7	0.8	1.76	●	●	●
1969	●	●	6.1	●	●	●	3.1	●	●
1970	●	●	7.8	●	●	●	4	●	●
1972	●	●	5.7	●	●	●	●	●	●
1974	●	●	4.4	●	●	●	0.89	●	●
1976	●	12.8	●	●	●	●	●	●	●
1977	13.8	12.2	5.4	●	●	●	●	●	●
1978	13.5	60.4 <sup>a</sup>	●	●	●	●	●	●	●
1979	●	48.0 <sup>b</sup>	●	●	●	●	●	●	12.5
1984	●	●	1	●	●	●	●	●	9.9
1991	●	●	1	●	●	●	●	●	●
1993	14.7	6.9	0	●	●	●	●	●	●
1996	●	●	0.3	2.9	3	2	2.4	12.3	6.7

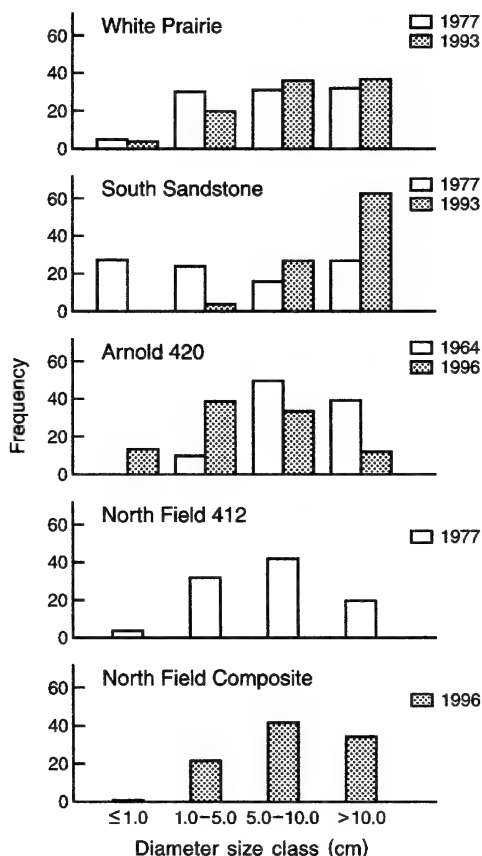


FIG. 1. Size structure of *Nassella* populations for different stands at Hastings Reservation. Plots in North Field were measured only once. Size structures of North Field plots 427, 428 and 429 did not differ and thus the composite of these three plots is shown.

and 1996. In North Field plot 428, *Nassella* density increased between 1944 and 1966, and although density in 1966 was very similar to that in 1996, measurement of the subplot of 428 (North Field 429) indicated that there were fluctuations in density over this time period. *Nassella* density in the two plots in Arnold Field changed in opposite directions. Arnold 420 had greater density in 1996 than in 1964. Density in Arnold 449 decreased from 1978 to 1996.

Size structure of *Nassella* populations varied between plots (Fig. 1). The White Prairie population showed little difference in size structure between 1977 and 1993 (Fig. 1). Numbers of individuals in the three larger size classes were approximately equal to each other, and about three times more numerous than individuals in the smallest size class. At South Sandstone, in 1977, the smallest size class and the largest size class contained roughly equal numbers of individuals, and the two intermediate size classes were only slightly less nu-

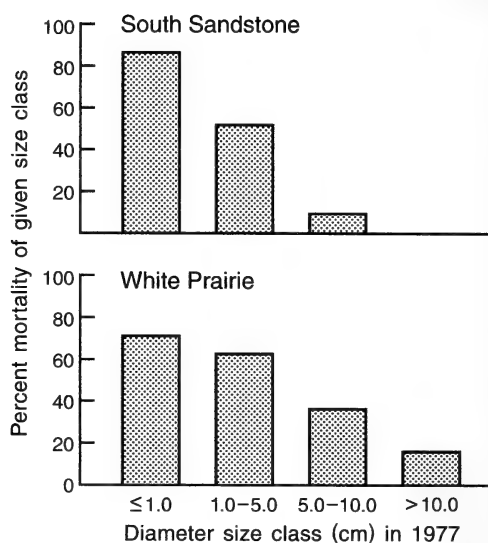


FIG. 2. Mortality as a percent of given size class for two *Nassella* populations at Hastings Reservation.

merous. However, in 1993, size structure of the stand had come to resemble White Prairie: the smallest size class had disappeared entirely, numbers of plants in the one to five cm size class had decreased significantly relative to 1977, and the larger two size classes increased in number. For North Field plots, it was not possible to determine changes in population size structure because we had only one observation for each plot. In 1977, North Field 412 (former vineyard) had the most *Nassella* individuals in the five to 10 cm size class, with fewer larger and smaller plants. Size structure in North Field 427, 428, and 429 in 1996 was very similar to that of White Prairie in 1993. Because size distributions of the three North Field plots were very similar, only a composite of these plots is shown. In 1964, Arnold 420 had most plants in the larger two size classes, with no plants in the smallest size class and very few in the one to five cm class. In 1996, the largest two size classes had decreased significantly, the smallest size class was represented, and the one to five cm size class was the largest.

Mortality patterns were very similar in the two plots (White Prairie and South Sandstone) for which individuals could be identified over time (Fig. 2). Most mortality between 1977 and 1993 was in the smallest size class, with decreasing percentage mortality for larger size classes. At South Sandstone, total mortality in the three larger size classes combined was only eight individuals. White Prairie showed only slightly greater mortality in the three larger size classes.

Seedling recruitment was sporadic in space and time (Table 4). No general pattern of recruitment connected to either yearly average rainfall or

TABLE 4. *NASSELLA* SEEDLING RECRUITMENT (SEEDLINGS/m<sup>2</sup>) FOR PLOTS AT HASTINGS RESERVATION. Missing entries indicate that plots were not yet established, or were not measured in that year.

Year	White Prairie	South Sandstone	North Field 412	North Field 427, 428, 429	North Field 409	Arnold 420
1964	•	•	0	•	0	0
1965	•	•	0.2	•	0	•
1969	•	•	4.0	•	0.2	•
1970	•	•	1.3	•	1.6	•
1972	•	•	0.2	•	•	•
1974	•	•	0.1	•	0	•
1976	•	13.1	•	•	•	•
1977	0.7	0.6	0.5	•	•	•
1978	0.8	49.8	•	•	•	•
1979	•	34.1	•	•	•	•
1984	•	•	0	•	•	•
1991	•	•	0	•	•	•
1993	0.7	0.1	0	•	•	•
1996	•	•	0	0.03	0.1	1.7

monthly average rainfall was found. In years with seedling recruitment, seedling mortality was very high the first spring, and declined with time (Fig. 3). At South Sandstone, eight of 131 small individuals noted in 1976 survived to 1993. Of the six *Nassella* seedlings noted in 1977, one survived to 1993. Although individuals recruited after 1977 were not followed between 1978 and 1993, 24 new individuals recruited into the South Sandstone population. At White Prairie, a comparison between maps made in 1977 and 1993 indicates 50 new individuals in the population. However, some of these are likely clonal fragments of previously existing individuals.

Minimum longevity measurements for *Nassella* were made using tagged individuals. At White Prairie, 38 plants tagged in 1977 could be unequivocally identified in 1993. Of these 38 individuals, 22 had increased in basal area over this 16-year period,

indicating that they were still vigorous after this amount of time. At South Sandstone, 69 plants were identified as being more than 17 years old, and of these, 51 had increased in basal area. At North Field 428, 12 plants were staked in 1966 and one of these was still alive thirty years later. At Arnold 449, 18 tags were re-located after 17 years, five of which still had living *Nassella* individuals.

Actual age of large *Nassella* individuals was estimated using the average rate of increase of basal area over a 16-year period (Table 5). Due to large variation, long-term average growth rates were not significantly different between size classes or between sites. The largest individuals at White Prairie and South Sandstone had basal areas between 400 and 700 cm<sup>2</sup>. Using the average long-term growth rate for both sites and all size classes (5.0 cm<sup>2</sup>/year), these individuals were calculated to be 80 to 140 years old.

Accumulation of dead material in individual *Nassella* tussocks does not predict individual mortality. In 1976, maps of the South Sandstone plot

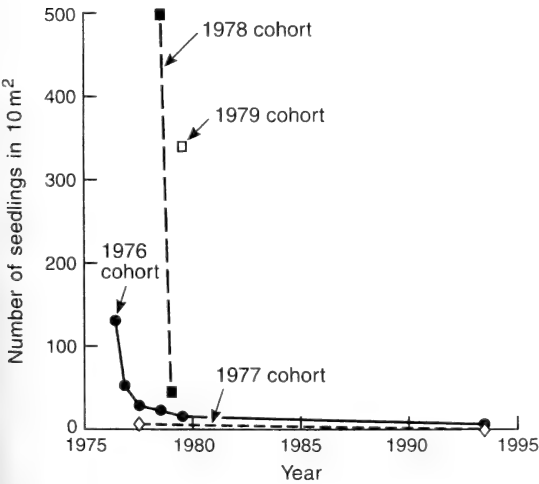


FIG. 3. Seedling mortality over time for four cohorts of seedlings at Hastings Reservation South Sandstone plot.

TABLE 5. INCREASE IN BASAL AREA BY SIZE CLASS (cm<sup>2</sup>/YEAR) OF *NASSELLA* IN PLOTS AT HASTINGS RESERVATION. Only plants that increased in size over time period are included. Data are averages  $\pm$  1 standard deviation. Numbers in parentheses are numbers of plants.

Beginning size class	White Prairie 1977 to 1993	South Sandstone 1976 to 1993
$\leq 1$ cm ( $\leq 0.78$ cm <sup>2</sup> )	none	$3.2 \pm 2.8$ (8)
1 cm to 5 cm ( $0.78$ to $19.6$ cm <sup>2</sup> )	$4.2 \pm 2.9$ (9)	$5.5 \pm 5.6$ (14)
5 cm to 10 cm ( $19.6$ to $78.5$ cm <sup>2</sup> )	$2.5 \pm 1.9$ (8)	$4.7 \pm 6.4$ (14)
$> 10$ cm ( $> 78$ cm <sup>2</sup> )	$8.5 \pm 6.8$ (4)	$6.1 \pm 5.9$ (15)

indicated 24 individuals that had large regions of dead material. In 1993, only two of these individuals had experienced large declines in living basal area. Between 1976 and 1993, many individuals that initially seemed to be senescing or fragmenting rebuilt their tussocks and increased in living basal area.

## DISCUSSION

### Landscape-scale Dynamics of *Nassella* Without Fire or Grazing

In general, *Nassella* bunchgrasses have increased at Hastings Reservation in the absence of fire and grazing. Both our data and those of White (1966) indicate that *Nassella* colonized new areas from 1944 to 1966 (Table 3). As *Nassella* has spread to new areas, total average basal cover in established stands has remained stable. In 1967, average basal cover of *Nassella* for 13 protected stands at Hastings Reservation was 10% (White 1967). For a subsample of these areas, we also found a total average basal cover of 10% in 1977 (White Prairie and South Sandstone) and again in the 1990's (White Prairie, South Sandstone, and Arnold Field). At finer resolution, we found a difference in plots that were historically cultivated and those that were not. In the 1990's, average basal cover in formerly cultivated plots was only about 4%, compared to 12% for plots that were never cultivated. The only location where *Nassella* has not maintained itself is in the former vineyard.

### Stand-scale Dynamics of *Nassella*

Non-native annuals are present in varying levels all these stands (Stromberg and Griffin 1996) and by themselves, did not seem to be sufficient to cause stand declines. At White Prairie, where the only known disturbance was the historical introduction of non-native annuals, (1971–1991 cover of non-native, annuals was 33.1%) there was essentially no change in basal cover, density, or size distribution of *Nassella* over a 16-year period of this study. It is possible that one or more of these measures showed a transient initial reaction to non-native annuals when they first became important in the 1800's. However, at another *Nassella* grassland site in California, micro-fossil evidence suggests that density, at least, has not been affected by non-natives (Bartolome et al. 1986).

Although non-native annuals did not appear to impact *Nassella*, even light grazing did cause significant changes in *Nassella* stands. Over the same period that the ungrazed *Nassella* stand at White Prairie was stable, the stand at South Sandstone, which had been formerly grazed, increased both in total basal cover and in changes in size distributions. By 1993, total *Nassella* basal cover at South Sandstone was indistinguishable from the relict White Prairie plot. This suggests that a basal cover

of around 1000 cm<sup>2</sup>/m<sup>2</sup> may be the maximum that can be supported in these stands at Hastings Reservation. Spacing of large individuals probably reflects long-term competition for water in limiting years, and for small individuals, competition with alien annual species (Dyer and Rice 1997, 1999).

Areas that were disturbed by soil cultivation supported stands with lower total cover of *Nassella*, and had size distributions that are qualitatively different from areas that were never cultivated. It is not clear whether cultivation was a disturbance that permanently altered the ability of areas to support *Nassella* stands (Stromberg and Kephart 1996), or whether recovery is simply extremely slow. However, there is little indication that stands in formerly cultivated areas are developing toward patterns similar to never-cultivated plots. Again, the only plot where *Nassella* disappeared was the site of the former vineyard.

It is possible that differences between cultivated and non-cultivated plots are due simply to pre-existing site differences from before 1900. However, both the White Prairie plot and the South Sandstone plot are associated with oak woodland, as was North Field originally. Furthermore, another study that included 80 sites from around Hastings Reservation and the Carmel Valley also concluded that *Nassella* and a number of other native plant species (e.g., *Poa secunda* J.S. Presl and *Chlorogalum pomeridianum* (DC.) Kunth) are rare in sites that have been subjected to historic cultivation (Stromberg and Griffin 1996).

### Life-stage Mortality of *Nassella* in the Presence of Non-native Annuals

We found that mortality was concentrated in the smaller size classes, and that initial seedling mortality was very high. Similar results were found in a study of individually marked *N. pulchra* in the San Joaquin valley of California (Marty 2002). Differential mortality of young plants is very common (Sarukhan et al. 1984 and references cited therein), and studies have also noted very high seedling mortality for *Nassella* (Bartolome and Gemmill 1981; Dyer et al. 1996). However, it is unclear both the degree to which interference (*sensu* Harper 1961; Muller 1969) is involved, and the relative importance of inter- versus intraspecific interference in this mortality. In plots where density of mature *Nassella* individuals was low, interspecific interference from non-native annuals is probably a primary factor leading to high seedling mortality and limiting seedling recruitment. Studies have shown explicitly that interference from non-native annuals is detrimental to performance of *Nassella* individuals (Nelson and Allen 1993; Dyer and Rice 1997; Hamilton et al. 1999). However, *N. pulchra* seedlings can recruit into areas dominated by non-native annuals, although competition for soil moisture greatly reduced their growth (Hamilton et al. 1999).

The ability of *Nassella* or other native, perennial grass seedlings to thrive in soil dominated by non-native annuals may be influenced by soil microbial communities. Robinson (1971) found that *Nassella* seeds planted in Hastings soils dominated by *Avena* had significantly lower survival and growth compared to seeds grown in soils from relict stands of *Nassella*. Steenwerth (2002) found that Hastings old fields, as well as nearby recently tilled fields of the similar soil, had dramatically different microbial communities compared to similar soils in undisturbed, relict *Nassella* stands. Indeed, a simple inoculum of soil from non-native grasslands appears to inhibit the growth of native California grasses (Subramaniam et al. 2001).

When basal cover of mature *Nassella* individuals is high, intraspecific interference may be more important than interspecific competition as a factor in *Nassella* seedling mortality. High seedling recruitment appeared to be associated with low basal cover of mature *Nassella* individuals (despite presence of non-native annuals) and declined as *Nassella* density increased. For South Sandstone in particular, as total basal cover of *Nassella* became similar to White Prairie, seedling recruitment densities became similar. Intraspecific competition for soil resources in established bunchgrass stands in semi-arid grasslands often causes seedling recruitment to be very low in the absence of disturbance (Aguilera and Lauenroth 1993b; Hook et al. 1994; Aguilera and Lauenroth 1995).

It has been suggested that the bunchgrass growth form may be inherently associated with an increasing risk of death as tussocks increase in size (Harper 1977). This could be due to accumulation of plant litter in the tussock in situations where grasses are not subjected to periodic fire or grazing. Thus, lack of fire or grazing could lead to senescence of adult *Nassella* individuals (Menke 1992). This does not appear to be the case for established stands at Hastings Reservation, an inland dry grassland co-dominated by *Nassella*. Mortality of large individuals in plots that were never cultivated was very low, despite the presence of non-native annuals. For example, South Sandstone showed no mortality in the largest size class and individuals that appeared to be fragmenting demonstrated the ability to rebuild the tussock. Indeed, tussock fragmentation is very common in perennial bunchgrasses (Wilhelm 1995), and individual tussocks would be expected to possess the ability to rebuild through activation of dormant meristems (Bell 1984; White 1984). There was a small amount of mortality among large individuals at White Prairie, but this was probably due, at least in part, to gopher activity (Stromberg and Griffin 1996) and did not impact total *Nassella* cover. In contrast, there was evidence of mortality of large individuals in formerly cultivated plots. It is possible that in these areas altered site conditions reduce longevity of *Nassella* individuals or that interference from non-native annuals is more detri-

mental in these locations. Gopher activity could also increase mortality of *Nassella*, and, while this might be important in Arnold Field, we observed little evidence of gophers in North Field. Responses to grazing in wetter, coastal California grasslands may be dramatically different (Stromberg et al. 2001) and longevity and responses to management may vary between inland and coastal California *Nassella* grasslands.

Contrary to some predictions (e.g., Menke 1992), tagged plants in our plots indicate that mature *Nassella* individuals are vigorous after as much as 30 years of protection from grazing and burning. Age of clonal plants, such as *Nassella*, is impossible to measure directly (Stebbins 1950), so use of rates of clonal spread to estimate age is commonly employed (e.g., Harberd 1961; Harberd 1962). Estimates of longevity of *Nassella* based on average growth rates indicate that large individuals are likely more than 100 years old. Because *Nassella* individuals break up into clonal fragments, as do many bunchgrasses (e.g., Lord 1993; Samuel and Hart 1995; Wilhelm 1995), individuals may persist in a series of clonal fragments much longer than this. In fact, clonal fragmentation is an alternative mechanism for recruitment of 'new' individuals into populations (Crampton 1974; Lord 1993). Although growth rates for individual clones can depend strongly on intraspecific competition (Aguilera and Lauenroth 1993a; Dyer and Rice 1997), interspecific competition (Nelson and Allen 1993; Dyer and Rice 1997; Hamilton et al. 1999), and genotype (Samuel and Hart 1995; Skalova et al. 1997), our age estimate is not unusually high. Studies of other species of bunchgrasses have also found that individuals can be very long-lived, with estimates ranging from 450 or 500 years or even longer in undisturbed areas (Coffin and Lauenroth 1988; Lord 1993; Lauenroth et al. 1994).

#### The Requirement for Management in *Nassella* Stands

Information on long-term population dynamics of native perennial grasses that have been left undisturbed by humans, is necessary to develop effective prescriptions for restoration and management of areas with native perennial grass stands. Large protected areas, such as Hastings Reservation, provide important reference systems in which to gather such information (Bock et al. 1993). Because there are no unaltered pre-European grassland communities remaining in California, there is no naturally occurring large model by which to establish goals or measure success of management or restoration efforts. Models for restoration of California native grasslands depend on observations of species dynamics in small patches. Such small patches may have been the common expression of native California grasslands and large homogenous stands of native grasses were rare. However, since



pre-European California grasslands probably contained many annual and perennial grasses and forbs (Heady 1977; Heady et al. 1992), one possible goal would be to promote overall diversity of native grassland species. This is complex because some management practices that could potentially benefit *Nassella* appear to be detrimental to other native bunchgrass species (Dennis 1989). Therefore, lacking detailed, species-specific information on the effects of potential management practices, landscape-scale management should be conservative. Because *Nassella* bunchgrasses that have been protected from grazing and burning show no signs of disappearing at the landscape scale at Hastings Reservation (despite the introduction of non-native annuals), landscape-scale management to maintain relict *Nassella* in the landscape appears to be unnecessary.

Stand-scale population dynamics are site dependent and appear to be related to land-use history; stand-scale management should take this into account. At Hastings Reservation, some of the bunchgrass stands probably pre-date European arrival, while other stands occur in sites that have been converted from other vegetation types such as oak woodland or chaparral. This is true for other areas of California as well (Huenneke 1989; Keeley 1993; Hamilton 1998). In areas that have never been cultivated, interference from non-native annuals does not seem to cause *Nassella* stand decline. Despite high seedling mortality and sporadic seedling recruitment, areas that were never cultivated can have high basal cover of *Nassella* and some achieve replacement levels of recruitment. Our longevity estimates, and the demonstrated ability of *Nassella* to repair dead portions of a tussock, suggest that many large *Nassella* individuals found in areas such as White Prairie and South Sandstone could have been present at Hastings Reservation before the area was first homesteaded in 1863 (White 1967). For such long-lived species, even if conditions allowing for seedling recruitment are quite rare, stands can achieve replacement recruitment (Noble 1986; Lauenroth et al. 1994). Thus, lack of seedlings is not necessarily an indication of future stand decline. *Nassella* stands in areas that have not been disturbed by cultivation do not appear to require management for maintenance.

Even light grazing appears to greatly reduce *Nassella* basal cover. Although *Nassella* can sometimes persist in grazed areas (White 1967; Stromberg and Griffin 1996), intensive, year-round grazing on inland stands seems to have the potential to be detrimental to stand persistence. More studies are required before decisions can be made concerning the compatibility of *Nassella* with grazers, or the use of grazing as a management tool as some have suggested (e.g., Menke 1992).

Cultivation appears to be the most detrimental disturbance, and left alone, *Nassella* seems to recover extremely slowly (if at all) from a distur-

bance of this type. Other studies have come to a similar conclusion (Stromberg and Griffin 1996). *Nassella* stands that were historically cultivated have low basal cover and do not appear to be developing toward the condition of stands that were not subjected to cultivation (e.g., Fig. 2). Furthermore, *Nassella* in at least one population in a historically cultivated stand has declined significantly. At Hastings Reservation, some of the *Nassella* stands that were historically cultivated occur in areas that have been converted to grassland from other vegetation types. In such cases, the appropriate management goal may be simply to promote *Nassella*. In formerly cultivated areas, there are few large individuals, and this suggests that *Nassella* may be shorter-lived in these areas than in areas that were never cultivated. Low basal cover in areas subjected to historic cultivation may be the result of seedling recruitment not being frequent enough for stand replacement or growth. Therefore, in areas with historical cultivation, active management to increase seedling survivorship, while not harming mature plants, may be required to increase abundance of *Nassella*.

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A NEW SPECIES OF *PRUNUS* (ROSACEAE) FROM THE MOJAVE DESERT  
OF CALIFORNIA

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ABSTRACT

*Prunus eremophila* (subgenus *Emplectocladus* Torr.) is described and illustrated from the southern Mojave Desert. It is closely related to *P. havardii* (W. Wight) S. C. Mason but differs from it in pubescence of leaves and larger size of floral parts and fruit.

Key Words: *Prunus*, *Prunus eremophila*, Rosaceae, Amygdaloideae.

During vegetation surveys of the Mojave Desert by the Bureau of Land Management (BLM), some unusual specimens of *Prunus* were collected by BLM botanists. After reviewing specimens of other woolly fruited species of *Prunus* at LA, RSA, GH, and UC and borrowing specimens of *P. havardii* from SRSC, it is concluded that they merit recognition as a new species.

***Prunus eremophila* Prigge, sp. nov. (Fig. 1).—**

TYPE: USA. California, San Bernardino Co. 12.8 mi NNW of Goffs on Lanfair Road and 0.8 mi E on road to True Blue Mine, 1145 m elev., 19 March 1992, *Prigge* 9825 (Holotype: RSA; Isotypes: CAS, GH, LA, MO, NY, TEX, UC).

*Pruno havardii* similis sed differt foliis villosis (non glabris vel subtiliter pubescentibus), hypanthio 3–6 mm longo (vs. 2.0–2.5 mm), sepalis 1.0–1.6 mm longis (vs. 0.5–1.0 mm), petalis 4–7 mm longis (non 2 mm longis vel carentibus), fructu lanato (non pubescenti vel canescenti) 10–16 mm long (vs. 7–10 mm) 9–11 mm lato (vs. 8–9 mm), et endocarpio 9–14 mm longo (vs. 6–9 mm).

Diocious,  $\pm$  globose to widely spreading, intricately branched shrubs to 2.2 m tall; outer bark on older stems gray glaucous becoming reddish brown; inner bark orange; branchlets grayish pubescent, weakly thorny but without sharp, indurated tips; internodes 3–14 mm long; short-shoot spurs 1.5–5 mm long. Leaves conduplicate in bud, spatulate to ovate, 5–20 mm long and 2–8 mm wide on short shoots, 13–30 mm long and 7–19 mm wide on long shoots, serrate (rarely entire or wavy) with a total of 0–13 teeth that are often asymmetrically disposed, sparsely villous on both surfaces, cuneate at base, acute, round, truncate, or retuse, often mucronulate at apex, lacking stomata on adaxial surface. Petioles 0.5–3.0 mm long on short shoot leaves, 2.0–5.0 mm long on long shoot leaves. Flowers axillary with 2–4 flowers per leaf axil, precocious, unisexual by abortion of either stamens or pistil. Hypanthium turbinate, pubescent externally,

strigose internally in male flowers, glabrous internally in female flowers. Sepals 5, 1.1–1.6 mm long, 1.4–2.3 mm wide, deltate, externally pubescent. Petals 5, white, 2.7–5.8 mm long, 2.2–4.0 mm wide, round to spatulate, slightly narrower and more acute in male flowers. Stamens 10–15, in 3 whorls of 5 stamens each or fewer by abortion, the uppermost whorl opposite the calyx lobes and originating on the hypanthium rim, the middle whorl opposite petals, the lowermost whorl  $\pm$  opposite the calyx lobes, with the lower two whorls of stamens arising from wall of hypanthium; filaments 1–2.6 mm long, white; anthers 0.7–1.2 mm long, 0.7–1.0 mm wide, light yellow. Pistil one (but occasionally two and then connate at the ovary), 4.8–6.0 mm long, the ovary 1.6–2.5 mm long, 1.5–1.8 mm in diameter, pubescent, the style 3.2–3.7 mm long. Fruit drupaceous, slightly laterally compressed ovoid to orbicular, (9–)11–16 mm long, (6–)8–11(–14) mm wide along major axis, (6–)7–10(–14) mm along minor axis, densely villous with grayish or rusty hairs; sarcocarp (exocarp + mesocarp) very slightly fleshy, ca 0.5 mm thick, easily separating from pit in fertile fruits but generally not split along the ventral suture, exocarp apricot color when ripe. Endocarp smooth, apiculate, and ventrally ridged, 9–15 mm long, 6–10 mm wide.

*Paratypes.* U.S.A. California. San Bernardino Co.: 12.8 road mi NNW of Goffs along Lanfair Road, then 0.8 mi E on trail-road toward Vontrigger Hills, 1160 m, 19 March 1992, *Henrickson* 22633 (CSLA); southern Lanfair Valley E of Bobcat Hills, 0.8 mi NE of True Blue Mine, 1145 m, 21 Mar 1980, *Prigge* 3634 (LA); Vontrigger Hills, 12.8 mi NNW of Goffs on Lanfair Road and ca. 1.95 air mi E of junction of Lanfair Rd and road to True Blue Mine, 1155 m, 3 Apr 1985, *Prigge* 6235 (LA, RSA); (same area) 7 May 1985, *Prigge*, *Thompson*, and *Davis* 6374 (NY, TEX, UC, RSA, CAS, GH); (same area) 19 March 1992, *Prigge* 9826 (TEX, RSA); (same area and date), *Henrickson* 22632 (CSLA); Lanfair Valley, 12.9 air mi N of Goffs

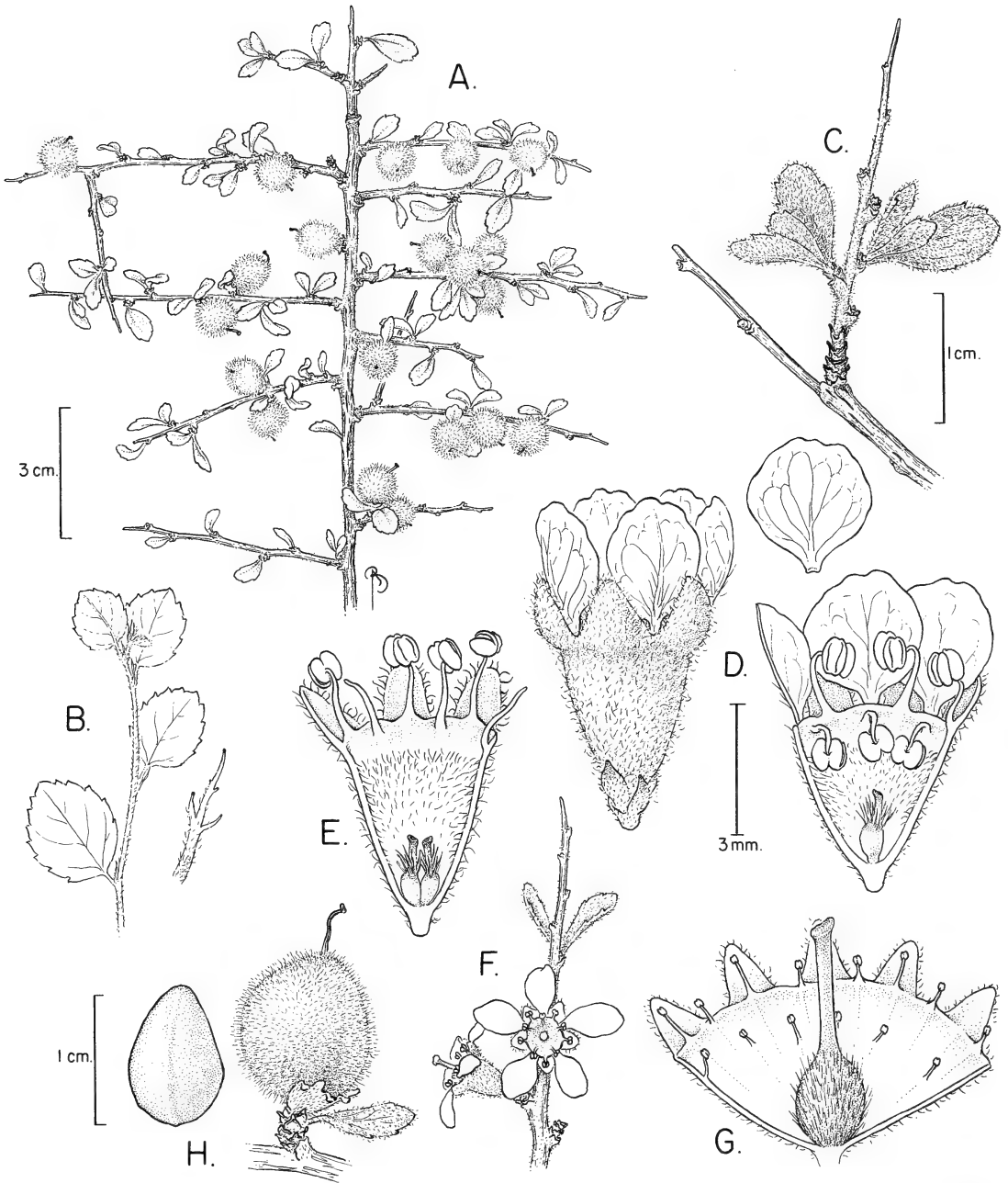


FIG. 1. *Prunus eremophila*: A) fruiting branch with short-shoot leaves (Prigge 6372); B) branch with long-shoot leaves and stipule; C) short-shoot leaves; D) male flower—early anthesis (left), dissected flower with rudimentary pistil (right), and petal (above); E) dissected male flower with two rudimentary pistils (abnormal); F) terminal branch with female flowers and rudimentary stamens; G) dissected female flower with rudimentary stamens; H) endocarp and fruit.

where Old Government Road crosses Sacramento Wash, 1165 m, 13 May 1992, Prigge and Henrickson 10220 (RSA).

*Prunus eremophila* occurs primarily in washes but also on rocky slopes in the higher zones of the creosote bush series and the transition zone from

creosote bush to the blackbush series where there are scattered Joshua trees (Sawyer and Keeler-Wolf 1995). Substrates are derived from igneous rocks (granites and rhyolites). Common associates are *Tetradymia stenolepis*, *Ericameria cooperi*, *Yucca brevifolia*, *Y. schidigera*, *Acamptopappus sphaero-*

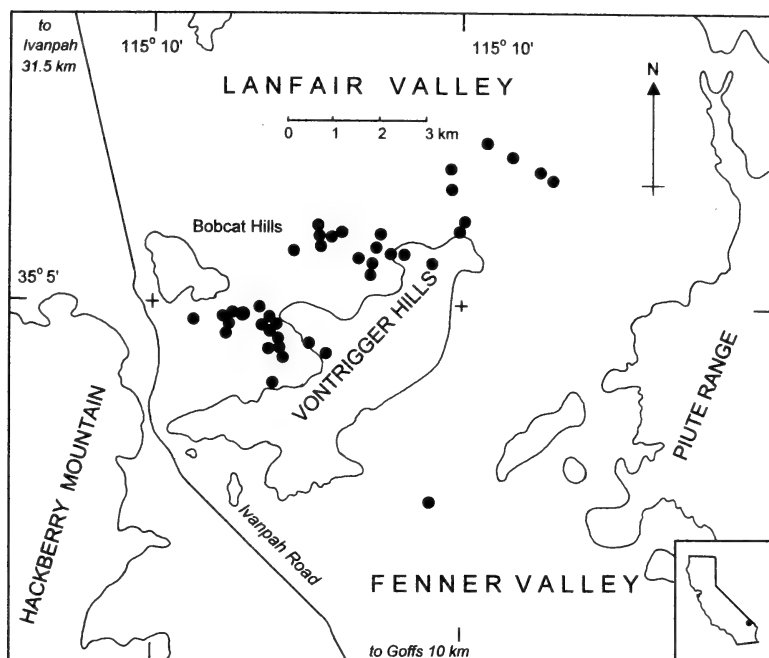


FIG. 2. Known distribution of *Prunus eremophila* (●) in eastern San Bernardino County, California.

*cephalus*, *Eriogonum fasciculatum*, *Larrea tridentata*, *Salazaria mexicana*, *Yucca baccata*, *Lycium oligosperma*, *Krameria erecta*, and *Xylorhiza tortifolia* (nomenclature follows Hickman 1993). Elevation ranges from 975–1175 m (3200–3850 ft). The species is known only from the vicinity of the Vontrigger Hills, Bob Cat Hills, southern Lanfair Valley, and one outlier in northeastern Fenner Valley of southeastern San Bernardino County (Fig. 2). Flowering time is from mid March to early April.

*Prunus eremophila* is in the subgenus *Emplectocladus* Torr. (commonly included in subgenus *Amygdalus* L.) as envisioned by Mason (1913). The subgenus is characterized by dioecy through abortion of stamens or pistils, a fine pubescence on the inside of the hypanthium, stamen number reduced to 10 or 15 with some filaments inserted on the hypanthial wall, and with or without stomata on the upper leaf surface (*Emplectocladus* and *Prunus* are the only subgenera of *Prunus* that have species without stomata on the upper leaf surfaces). All these traits, including the absence of adaxial leaf stomata, occur in *P. eremophila*. When Mason studied this subgenus, only four species (all North American) were known: *Prunus fasciculata* (Torr.) Gray, *P. microphylla* (H.B.K.) Hemsl., *P. minutiflora* Engelm., and *P. havardii*. With the description of *P. cercocarpifolia* from the Chihuahuan Desert region by Villarreal (1989) and now *P. eremophila*, the subgenus now consists of six species.

A comparison of vegetative, floral, and fruit characters among the species of *Emplectocladus* point to a possible close relationship between *Pru-*

*nus eremophila* and *P. havardii* of the Chihuahuan Desert of southwest Texas and northern Mexico and, to a lesser degree, with *P. microphylla* of central Mexico (states of San Luis Potosí, Hidalgo, México, and District Federal). *Prunus havardii* is thorny and has glabrous or sparsely pubescent leaves, and *P. eremophila* is only rigidly branched, not truly thorny and has villous leaves. The larger flower size (longer hypanthium length, longer petals, stamens, and pistils) and slightly larger fruit size of *P. eremophila* are distinctive within the subgenus *Emplectocladus* indicating that *P. eremophila* is distinctive and recognizable as a distinct species.

*Prunus eremophila* is sympatric with *P. fasciculata* but flowering time overlaps only partially. The former begins flowering about two to three weeks earlier than the latter, so that *P. eremophila* has almost completed flowering by the time *P. fasciculata* begins. There is a slight overlap in flowering (perhaps as much as a week) when cross pollination could occur between these two sympatric species, but no hybrids were found suggesting that additional isolating mechanisms other than seasonal ones are present.

At the present, the species does not appear to be threatened, but any species with such a limited distribution and small size (perhaps ca. 2000 individuals) could become threatened fairly quickly from off-road vehicle (ORV) use, grazing pressure, and mining activities or global warming. All known populations are within the recently formed East Mojave National Preserve, and the Preserve should

minimize or eliminate most threats from human activities. Future ecological and physiological studies to determine the population size and structure, seed germination requirements, seedling survival, recruitment, and threats would provide valuable data for evaluating the long term survivability of this species.

*Prunus eremophila* can be identified by making the following modification to the key in *The Jepson Manual* (Hickman 1993):

- 5' Twigs rigid; ovary and fruit generally densely puberulent.
  - 9. Flowers perfect; leaf blades glabrous (sometimes minutely puberulent on petiole, midrib, and basal margin in *P. fremontii*) and more than 3 mm wide.
    - 10. Leaf blades ovate to round, 7–22 mm wide, base obtuse to  $\pm$  cordate; petals white . . . . . *P. fremontii*
    - 10' Leaf blades elliptic to oblanceolate, base tapered; petals reddish . . . . *P. andersonii*
  - 9' Flowers imperfect; leaf blades glabrous to villous, if glabrous the leaf blades less than 3 mm wide.
    - 11. Leaf blades spatulate, 1–3 mm wide; puberulent or glabrous . . . . *P. fasciculata*
    - 12. Leaf surface puberulent; inland . . . . . var. *fasciculata*

- 12' Leaf surface glabrous to low-papillate; coastal . . . . . var. *punctata*
- 11' Leaf blades ovate, 2–19 mm wide, sparsely villous . . . . . *P. eremophila*

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A NEW *CEANOTHUS* (RHAMNACEAE) SPECIES FROM NORTHERN  
BAJA CALIFORNIA, MEXICO

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ABSTRACT

*Ceanothus bolensis* S. Boyd & J. Keeley is a new species in the subgenus *Cerastes* from northwestern Baja California, Mexico. It is well represented at elevations above 1000 m on Cerro Bola, a basaltic peak approximately 35 km south of the U.S./Mexican border. It is characterized by small, obovate to oblanceolate, cupped, essentially glabrous leaves with sparsely toothed margins, pale blue flowers, and globose fruits lacking horns. Principal components analysis on morphological traits shows it to be distinct from other members of *Cerastes* which are distributed away from the coast in southern California and Baja California, Mexico. These phenetic comparisons also suggest that *Ceanothus otayensis* should not be subsumed under *C. crassifolius*, as treated in the Jepson Manual, but rather should be retained at specific rank as well.

RESUMEN

*Ceanothus bolensis* S. Boyd & J. Keeley es una nueva especie del subgénero *Cerastes* en el noroeste de Baja California, México. Esta bien representada en altitudes por arriba de los 1000 m en el Cerro Bola, un pico basáltico, aproximadamente a 35 km de la frontera de USA/México. Esta se caracteriza por hojas pequeñas, obovadas a oblanceoladas, convexas, esencialmente glabras y con márgenes esparcidamente dentados, flores azul pálido y frutos globosos sin cornículos. El análisis de componentes principales con caracteres morfológicos la presenta como distinta de otros miembros de *Cerastes* distribuidos lejos de la costa en el sur de California y de Baja California, México. La comparación fenética también sugiere que *Ceanothus otayensis* no debe ser incluida dentro de *C. crassifolius* como en el Manual de Jepson, sino más bien debería ser retenida a nivel especie.

Key Words: *Ceanothus*, subgenus *Cerastes*, Baja California, Mexico, phenetic analysis, endemic.

*Ceanothus* is a diverse genus of shrubs with the center of species diversity in the Mediterranean-climate California Floristic Province (Schmitt 1993; source for nomenclature, except where indicated). It comprises approximately 60 species (van Renssalaer and McMinn 1942) more or less equally divided into two clades that have long been systematically recognized as subgenera *Ceanothus* and *Cerastes* (Harding et al. 2000).

Recent collections of a *Ceanothus* from northern Baja California, Mexico suggest a new taxon that is worthy of recognition. These collections are from Cerro Bola, a basaltic mountain, approximately 35 km south of the Tecate border crossing. At elevations between 1000 m and the peak at 1290 m, a small-leaved, erect, divaricately branched *Ceanothus* species in the subgenus *Cerastes* is frequent in chaparral dominated by

*Arctostaphylos glandulosa* Eastw. ssp. *adamsii* (Munz) Munz and *Chamaebatia australis* (Brandegee) Abrams. It is less frequent on lower slopes from at least 500 m elevation. This *Ceanothus* shares features with several other *Cerastes* species distributed in southern California and adjacent Baja California, Mexico. The lack of fruiting horns and deeply concave, toothed leaves suggests an affinity with *Ceanothus greggii* A. Gray var. *perplexans* (Trel.) Jepson and with the relatively recently described *C. ophiochilus* Boyd, Ross, & Arnseth (Boyd et al. 1991), a rare endemic in southwestern Riverside County. The small leaf size of the Cerro Bola plants is similar to *C. ophiochilus* and *C. otayensis* McMinn (van Renssalaer and McMinn 1942), a localized endemic on two mountain peaks in southern San Diego County, California and immediately adja-

cent Baja California, ca. 30–35 km northeast of Cerro Bola. In the most recent floristic treatment *C. otayensis* is treated as a hybrid derivative of *C. crassifolius* Torr., a widespread species away from the coast in southern California and Baja California, and *C. greggii* var. *perplexans*, the principle *Cerastes* species from the interior slopes of the Peninsular Ranges (Schmitt 1993).

METHODS

Herbarium specimens of the Cerro Bola taxon and other *Ceanothus* species in subgenus *Cerastes* from southern California were used for phenetic comparisons. Because fruit morphology has more distinguishing characters than flowers, only fruiting specimens were selected. Species used for comparison were *Ceanothus greggii* var. *perplexans*, *C. greggii* var. *vestitus* (Greene) McMinn, *C. ophiochilus*, *C. otayensis*, and *C. crassifolius*.

We selected 14 characters for analysis; 6 continuous quantitative, 7 qualitative and 1 calculated ratio (Table 1). For quantitative characters, two samples were measured for each specimen and the mean was used in the analysis. For qualitative characters, characteristics were given a relative score from 1 to 5. All character states were standardized as z-scores by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. A species matrix of these scores was used for ordination with principal components analysis using SYSTAT 5.05 (Evans-ton, IL).

RESULTS

Means values for phenetic characters for all taxa discussed above are shown in Table 1. The Cerro Bola specimens have the smallest leaves but they are not significantly different from the other two small-leaved taxa, *C. ophiochilus* and *C. otayensis*. Cerro Bola plants are similar to *C. ophiochilus* in their very deeply concave leaves, limited pubescence, and smaller fruits that lack horns, however, these two taxa differ in their leaf shape, reflected in the leaf length/width ratio. The broad leaves of Cerro Bola plants are quite unlike the nearly linear leaves of *C. ophiochilus*, which generates a length/width ratio roughly double that of all other taxa. The low apical angle on leaves of Cerro Bola plants is quite unlike *C. ophiochilus* but similar to *C. otayensis* and *C. greggii* var. *perplexans*. *Ceanothus otayensis* separates from all other taxa, except *C. crassifolius*, in having revolute leaves, well developed, often brownish pubescence on branchlets and undersides of leaves.

The principal components analysis for all taxa (Fig. 1), explained 50% of the total variance on the factor 1 axis and 20% on the factor 2 axis. *Ceanothus crassifolius* was widely separated from the other taxa on the factor 1 axis; the most important components being convex leaves, revolute margins,

TABLE 1. LEAF AND FRUIT COMPARISON OF *CEANOTHUS BOLENSIS* AND OTHER SPECIES IN SUBG. *CERASTES* (X ± SD).

Character	<i>C. bolensis</i>	<i>C. greggii</i> var. <i>perplexans</i>	<i>C. greggii</i> var. <i>vestitus</i>	<i>C. ophiochilus</i>	<i>C. otayensis</i>	<i>C. crassifolius</i>
n	26	9	7	12	12	10
Leaf length (mm)	4.9 ± 0.8	14.7 ± 2.6	10.1 ± 2.4	5.2 ± 0.8	7.1 ± 1.7	23.0 ± 4.4
Leaf width (mm)	3.9 ± 0.7	12.2 ± 1.9	5.9 ± 1.8	1.7 ± 0.5	5.2 ± 1.2	12.1 ± 2.6
Length/width ratio	1.3 ± 0.2	1.2 ± 0.1	1.8 ± 0.4	3.2 ± 1.1	1.4 ± 0.2	1.9 ± 0.3
Leaves concave (1 = no, 5 = extreme)	4.3 ± 0.7	2.9 ± 0.6	3.3 ± 0.3	4.5 ± 0.5	3.2 ± 0.5	1.0 ± 0.0
Leaves revolute (1 = no, 5 = extreme)	1.0 ± 0	1.1 ± 0.2	1.0 ± 0	1.0 ± 0.0	3.8 ± 0.8	4.6 ± 0.7
Teeth on leaves (1 = none, 5 = many)	3.4 ± 0.7	3.8 ± 0.6	1.8 ± 1.1	1.3 ± 0.7	3.5 ± 0.4	2.8 ± 1.1
Apical angle of leaves (°)	4.8 ± 5.1	6.7 ± 4.3	37.5 ± 11.8	24.2 ± 7.3	5.2 ± 5.6	29.5 ± 15.3
Basal angle of leaves (°)	50.1 ± 13.6	37.5 ± 20.0	54.6 ± 17.3	77.5 ± 4.1	57.7 ± 7.3	50.5 ± 10.3
Pubescence on branchlets						
(1 = glabrous, 5 = dense)	2.6 ± 0.5	3.3 ± 0.9	3.6 ± 0.5	2.1 ± 0.3	4.4 ± 0.5	5.0 ± 0.0
Pubescence on leaf abaxial side						
(1 = glabrous, 5 = dense)	1.0 ± 0.0	1.7 ± 1.0	2.7 ± 0.5	1.0 ± 0.0	4.3 ± 0.5	4.9 ± 0.3



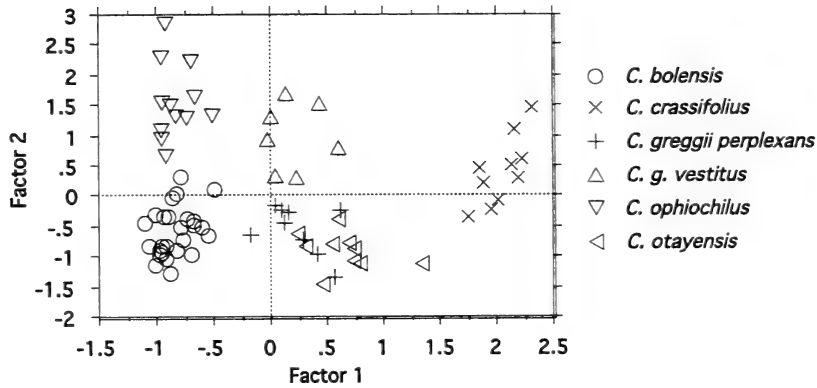


FIG. 1. Principal components analysis of *Ceanothus crassifolius*, *C. greggii* var. *perplexans*, *C. greggii* var. *vestitus*, *C. otayensis*, *C. ophiochilus*, and *C. bolensis*. Factor loading scores are in Table 2.

leaf length, pubescence characters and fruit horns (Table 2). *Ceanothus otayensis* was clearly separated from *C. crassifolius* on both the factor 1 and factor 2 axes but overlapped with *C. greggii* var. *perplexans* (Fig. 1).

Taking *C. crassifolius* out of the analysis gave greater resolution to the separation of *C. otayensis* and *C. greggii* var. *perplexans* (Fig. 2). In this analysis, factors 1 and 2 explained 36% and 21%, respectively of the total variance. *Ceanothus otayensis* was most prominently separated along the factor 1 axis, where pubescence characters and degree of leaf concavity were among the important components. On the factor 1 axis the Cerro Bola plants were distinctly intermediate to *C. otayensis* and *C. ophiochilus*. Cerro Bola plants were distinctly separated from *C. greggii* varieties on the factor 2 axis, where the important components were pedicel length, fruit horns, leaf length and apical angle (Table 2). Clearly there is a sound morphological basis for the recognition of the Cer-

ro Bola taxon (Figs. 1, 2), treated here as a new species.

SPECIES TREATMENT

***Ceanothus bolensis*** S. Boyd and J. Keeley, sp. nov. (Fig. 3)—TYPE: MEXICO, Baja California, chaparral with *Chamaebatia australis* on NE side of Cerro Bola, S of Tecate, elevation 1000 m, 26 Apr 1996, Jon E. Keeley 27233 (RSA).

Differt a *C. ophiochilus* foliis late obovatis vel late oblanceolatis; a *C. otayensis* foliis glabris, non concavis, marginibus revolutis; a *C. greggii* var. *perplexans* foliis glabris, parvulis (sub 6 mm longis).

Erect, divaricately branched shrub, 1–1.5 m tall, lacking basal burl and not resprouting after top-killed. Older stems ashy gray, intricately branched with rigid diverging branches. Younger branches reddish gray and lightly puberulent. Stipules thick-

TABLE 2. CHARACTERS USED IN PHENETIC ANALYSIS AND FACTOR LOADINGS FOR PRINCIPAL COMPONENTS ANALYSIS FOR FIGURES 1 AND 2.

Character	Figure 1		Figure 2	
	Factor 1	Factor 2	Factor 1	Factor 2
Leaf length	0.88	0.04	0.64	0.60
Leaf width	0.78	-0.25	0.71	0.30
Length/width ratio	-0.08	0.86	-0.504	0.460
Leaves revolute	0.83	-0.06	0.66	-0.39
Leaves concave	-0.92	0.04	-0.78	-0.24
Teeth on leaves	0.11	-0.84	0.52	-0.52
Apical angle of leaves	0.35	0.77	-0.25	0.73
Basal angle of leaves	-0.22	0.70	-0.44	0.17
Pubescence on branchlets	0.88	-0.17	0.84	-0.10
Pubescence on bottom of leaves	0.88	-0.03	0.77	-0.11
Pubescence includes brown hairs	0.78	-0.13	0.66	-0.41
Pedicel length	0.67	0.31	0.36	0.81
Fruit width	0.76	0.13	0.42	0.17
Presence of fruit horns	0.82	0.27	0.49	0.63

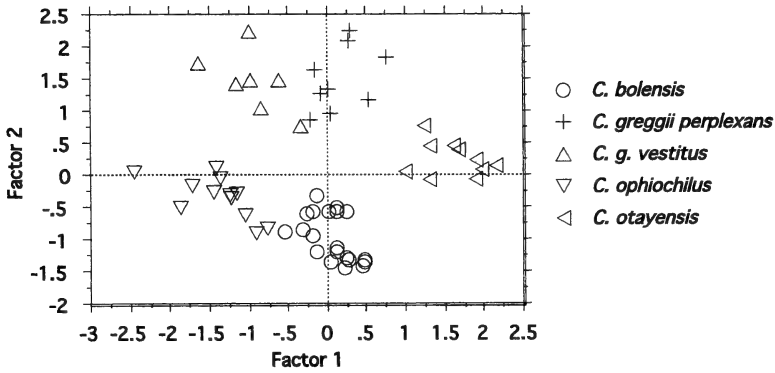


FIG. 2. Principal components analysis without *Ceanothus crassifolius*, but including all other taxa considered in Fig. 1. Factor loading scores are in Table 2.

ened and persistent, waxy or corky, dark reddish brown to purplish black. Leaves evergreen, thick, coriaceous, yellowish green, opposite, often clustered on short axillary spur branches; petioles 0.5–1 mm long,  $\pm 0.4$  mm wide, minutely puberulent; blades broadly obovate to oblanceolate, deeply concave, (2.5)4–6(10) mm long and (3)4–7(9) mm wide, surfaces sparsely puberulent when young, glabrate in age, margins not revolute, sharply dentate distally with (1)2–3 pairs of lateral teeth and an apical tooth; midvein prominent abaxially, lateral veins obscure, 3–5 pairs. Inflorescence a subumbellate axillary raceme, peduncle  $\pm 2$  mm long, densely short puberulent, bearing 6–8 flowers. Calyx, including receptacular disk  $\pm 5$  mm wide at anthesis, lobes 5, pale blue, fading cream-white, 1.8–2 mm long, deltoid to ovate, apex acute. Petals 5, pale blue, fading cream-white, 1.8–2 mm long, ladle-shaped,  $\pm$  equally divided into deeply saccate distal blade and filiform proximal claw. Stamens 5, filament 1.8–2 mm long, anther  $\pm 0.4$  mm. Ovary with style 1.8–2 mm long, 3-lobed, the lobes  $\pm 0.4$  mm; fruit a globose to depressed globose capsule, dark green to reddish, 3–4 mm diameter, smooth, lacking apical horns, lateral valve crests absent or vestigial.

**Distribution.** At present, *Ceanothus bolensis* is known only from the mid- to upper slopes of Cerro Bola ( $>500$  m), where it is locally common in the chaparral vegetation. To our knowledge, no other member of subgenus *Cerastes* is found on the mountain, and plants are uniform in overall gross morphology. Cerro Bola is noteworthy as a station for several other phytogeographically interesting taxa, such as the near-endemic *Arctostaphylos bolensis* P. V. Wells, as well as *Ceanothus papillosus* Torr. var. *roweanus* McMin and *Lepechinia cardiophylla* Epling, two taxa considerably disjunct from their previously known occurrences in the Santa Ana Mountains of Orange and

Riverside counties, California (Boyd et al. in prep).

**Paratypes.** MEXICO, Baja California, chaparral with *Chamaebatia australis* on NE side of Cerro Bola, S of Tecate, elevation 1000 m, 26 Apr 1996, Jon E. Keeley 27232 (BCMEX); ibid, Jon E. Keeley 27227 (CAS); ibid, Jon E. Keeley 27234 (SD); ibid, Jon E. Keeley 27238 (US); ibid, Jon E. Keeley 27236 (MEXU); occasional in chaparral on north slope of Cerro Bola, seen to summit (1275 m), near 31°19.5'N, 116°40'W, elevation ca. 550 m, 6 Jun 1970, Reid Moran 17780 (RSA, SD).

#### RELATIONSHIPS

*Ceanothus bolensis* shows a marked morphological similarity to several other members of subgenus *Cerastes* in the southern California region. It is most distinct from the widespread *C. greggii* var. *perplexans* by having very small leaves that are deeply concave. These two leaf traits bear a strong resemblance to *C. ophiophilus*, however, leaf shape is markedly different, with the latter species being more similar in leaf shape to *C. greggii* var. *vestitus*.

*Ceanothus bolensis* is quite distinct from another local endemic, *C. otayensis*, a taxon restricted to a few mountain peaks about 30–35 km northwest of Cerro Bola. *Ceanothus otayensis* has been subsumed under *C. crassifolius* (Schmitt 1993) due to the presence of several shared morphological similarities (revolute leaves and dense pubescence that includes brown hairs). Munz (1959) likewise treated *C. otayensis* as *C. xotayensis* McMin, and suggested it was probably a hybrid between *C. crassifolius* and *C. greggii* var. *perplexans*. However, principal component analysis on all 14 traits shows *C. otayensis* to be quite distinct from *C. crassifolius* (Fig. 1) and distinct from *C. greggii* (Fig. 2). Extensive exploration of both known southern California localities of *C. otayensis*, the upper slopes of Otay Mtn. (1090 m) and San Miguel Mtn. (780 m),

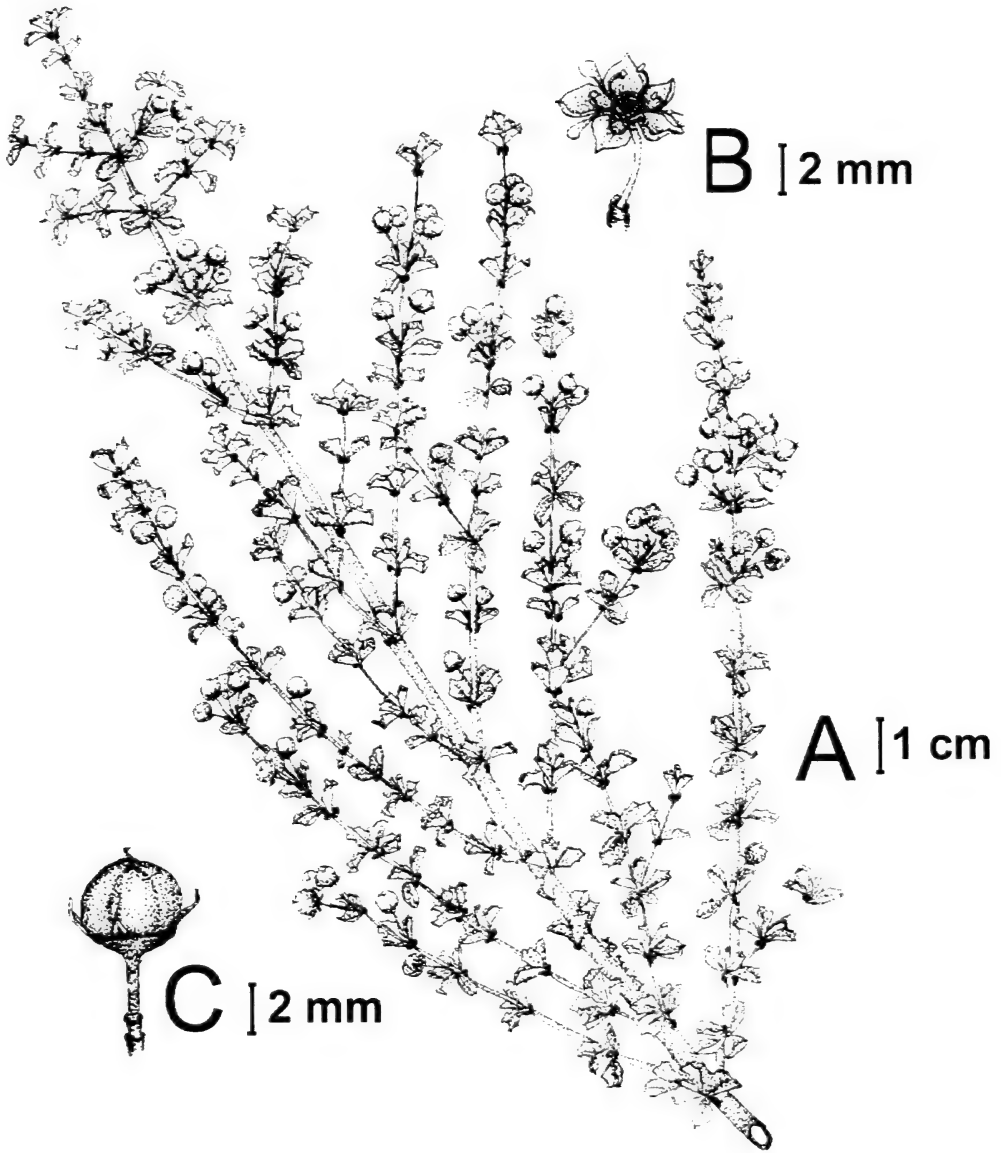


FIG. 3. *Ceanothus bolensis*. A. Fruiting branch showing characteristic small, toothed leaves, and hornless fruits on short axillary peduncles. B. Detail of individual flower. C. Detail of mature capsule showing absence of apical or lateral horns. (Illustrations by Melanie Baer-Keeley.)

failed to uncover populations of either *C. greggii* or *C. crassifolius*. *Ceanothus otayensis* forms homogenous populations that appear to be breeding true and lack any indication they are unstable hybrid swarms (J. Keeley unpublished observations). In addition to the naming of *C. bolensis*, we suggest *C. otayensis* be recognized at the specific rank as described by McMinn (van Rensselaer and McMinn 1942).

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NOTE

*COLLINSIA ANTONINA* IS EVOLUTIONARILY DISTINCT FROM *C. PARRYI*  
(SCROPHULARIACEAE SENSU LATO)

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A diminutive blue-eyed Mary from shale exposures in the San Antonio Hills (Santa Lucia Range) of southern Monterey County, California, was described by Hardham (1964) as *Collinsia antonina*. Plants assigned to *C. antonina* resemble members of *C. parryi* A. Gray, from the Transverse Ranges of southern California, and have been treated as either close relatives (Munz 1968) or, most recently, as members (Neese 1993) of *C. parryi*. The considerable disjunction between populations in the Santa Lucia and Transverse ranges, although not unique [e.g., *Syntrichopappus lemmonii* (A. Gray) A. Gray (Compositae)], warrants closer scrutiny.

In our evolutionary investigations of Collinsieae, we have examined phylogenetic relationships among taxa throughout the tribe using sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA (see Armbruster et al. 2002). Upon including plants referable to *C. antonina* [E. C. Neese 21500 (JEPS)] in our analyses, we were surprised to find that members of *C. parryi* sensu stricto (s.s.) [E. C. Neese 21530 (JEPS)] appear to be more closely related to members of *C. concolor* Greene [E. C. Neese 21539A (JEPS)] than to members of *C. antonina*. *Collinsia concolor* and *C. parryi* s.s. constitute a strongly supported (99% bootstrap) clade, to the exclusion of *C. antonina* (Fig. 1). *Collinsia concolor* and *C. parryi* s.s. are both endemic to the southern California Floristic Province and differ greatly in inflorescence architecture and flower size (Table 1). Based on the tree topology presented in Fig. 1, small flower size may be a shared, ancestral characteristic of *C. antonina* and *C. parryi*, with large flowers being a derived feature of *C. concolor*. Such major shifts in flower size have occurred repeatedly throughout the evolutionary history of *Collinsia* (Armbruster et al. 2002).

Evolutionary distinctiveness of *C. antonina* and *C. parryi* s.s. is also reflected by differences in morphological characteristics (Table 1). In keys to species of *Collinsia* (e.g., Newsom 1929), *C. antonina* might be confused with the distantly related *C. childii* Parry ex A. Gray because both taxa have glandular inflorescences and small flowers and both occur in the Santa Lucia Range. The two taxa can be readily distinguished by differences in seed number per capsule (Table 1). Hardham (1964) recognized two sympatric subspecies of *C. antonina* (*C. a.* subsp. *antonina* and *C. a.* subsp. *purpurea* Hardham), which await further systematic evaluation.

*Collinsia antonina* warrants recognition as a distinct species based on the above molecular and morphological evidence. This narrowly endemic taxon was earlier considered rare and endangered by the California Native Plant Society (CNPS) (Smith and Berg 1988); since 1993, CNPS has followed Neese's (1993) treatment of Californian members of *Collinsia* by including *C. antonina* within the circumscription of the common species, *C. parryi* (Skinner and Pavlik 1994; California Native Plant Society 2001). In light of our findings, *C. antonina* deserves renewed attention by plant conservationists.

ACKNOWLEDGMENTS

We thank Elizabeth Chase Neese for her invaluable field collecting, taxonomic insights, and review of the manuscript, Bridget L. Wessa for extensive laboratory assistance, and reviewers Noel H. Holmgren, David J. Keil, and John L. Strother for helpful suggestions. This research was supported by grants from the Lawrence R. Heckard Endowment Fund of the Jepson Herbarium (to BGB), the Norwegian Research Council (to WSA), and NSF DEB-9708333 (to WSA).

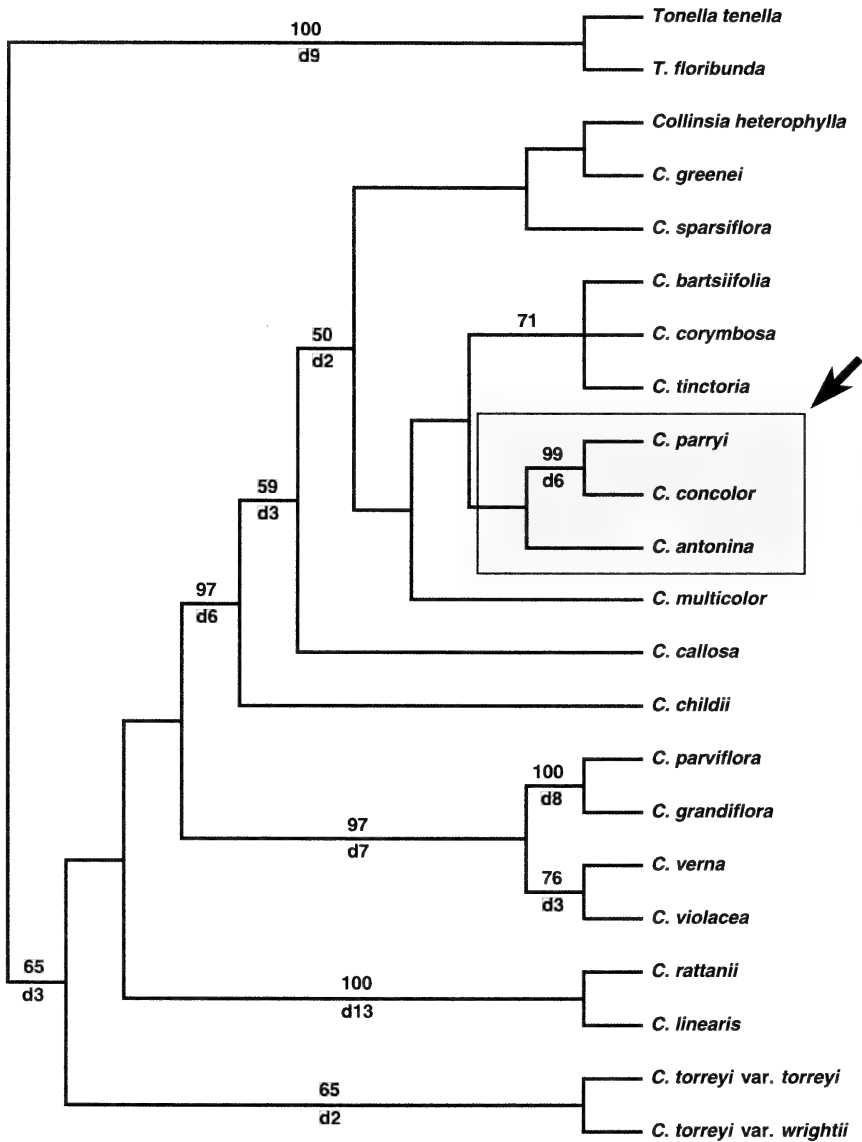


FIG. 1. The most parsimonious tree from phylogenetic analysis of nuclear ribosomal DNA sequences of the internal transcribed spacer region in tribe Collinsieae (Baldwin et al. unpublished; see Armbruster et al. 2002). The tree was rooted with sequences from outgroup taxa in tribe Cheloneae (*Chelone*, *Keckiella*, and *Penstemon*). Numbers above branches are bootstrap values (only values ≥ 50% are shown); numbers below branches, preceded by "d", are decay values (only values > d1 are shown). The clade including *Collinsia antonina*, *C. concolor*, and *C. parryi* is highlighted.

TABLE 1. SOME MORPHOLOGICAL DIFFERENCES BETWEEN *COLLINSIA ANTONINA* AND SIMILAR OR CLOSELY RELATED SPECIES.

	<i>C. antonina</i>	<i>C. parryi</i>	<i>C. concolor</i>	<i>C. childii</i>
Inflorescence glandularity	glandular	eglandular	glandular or eglandular	glandular
Longest-leaf length	5–10 mm	(5–)10–45 mm	10–45 mm	10–50 mm
Pedicle length	<10 mm	(5–)10–45 mm	1–5 mm	5–25 mm
Corolla length	6–7 mm	(5–)7–10 mm	10–16 mm	6–8 mm
Corolla color	white or purple	lavender-blue	blue/lavender-blue and white	pale lavender or white
Seeds/fruit	6–8	8–12	11–12	2

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## REVIEW

*Field guide to liverwort genera of Pacific North America*, by W.B. Schofield. 2002. Global Forest Society in association with the University of Washington Press, San Francisco, CA. 232 pp., 93 line drawings, glossary, and index. 7" × 10". \$25.00. ISBN 0-295-98194-6. Available at [www.washington.edu/press](http://www.washington.edu/press)

Most of the liverwort field guides and other taxonomic treatments covering this group of organisms in North America have focused primarily east of the 100th Meridian. It is therefore most welcome that this field guide covers much of the geographical area of interest to Madroño readers. This paperback book, while not quite a size to readily carry in the field, is nonetheless not heavy or excessively bulky. What we do have here is a well-designed volume. Bryophytes, the first land plants, are arranged into three lineages. The liverworts (and hornworts) are clearly less well known to most vascular-trained botanists than are the mosses. This volume is easy to use and will expand one's knowledge about this group of land plants. In some ways, this is a companion work to Schofield's field guide of *Some common mosses of British Columbia* published back in 1969. The Introduction to the liverwort genera field guide covers the first 22 pages and is concise yet very informative. The Introduction addresses how to collect liverworts and hornworts, followed by a short overview of collecting history of liverworts in Alaska, British Columbia, Washington, Oregon and California. Habitats, seasonality of finding liverworts, and distribution patterns in the region follow. Implications of liverworts to people end the Introduction section.

In most field guides, it is the illustrations and keys that determine how useful the book will actually be, especially to someone approaching the group for the first time. In this regard Schofield's book shines. While all keys have caveats about their use, I personally found the keys to be rather easy to use. The keys keep jargon and bryological terms to a basic minimum, and the couplets are succinct. The couplet choice is designed without a lot of overlapping characters. In many cases, genera key out in multiple places to accommodate the diversity of species within larger liverwort genera. The key itself is divided into eight sub-key sections to further expedite the identification process. Each genus is arranged alphabetically so it is easy to locate, and each genus has a full-page illustration. The illustrations are visually attractive and designed to represent a genus without being too technical. In some ways, they are more "artistic" than a detailed illustration, such as would be used in describing a new taxon. Actually, I think the illustrations provided are more effective as a represen-

tation at the genus level. Since liverworts are generally small plants, the bar scale provided with each illustration is important to review so one has a better idea of the organism's actual size.

A template is provided for each genus so comparisons can be made readily among closely related genera. Each genus has a short explanation about the meaning of its name, a statement of the number of species in the genus, its habit, its habitat, reproduction, local distribution, world distribution, distinguishing characteristics and similar genera.

The genera of hornworts within the Pacific North America are also included, adding further to the value of this book since one could confuse a hornwort for a thallose liverwort. However, hornworts upon closer examination can readily be distinguished from the liverworts, especially when sporophytes are present. The determination of the two hornwort genera covered in the book, occurs at couplet 28 of key II. Another interesting feature, and I think a great decision, is adding *Takakia* (Takakiaceae) to the book. The placement of this genus within the bryophytes has been a considerable puzzle, with some specialists insisting it is a liverwort while others opted to say it was more closely aligned with the mosses. Although it has been finally determined to be basal to the moss lineage (based on the sporophyte), it clearly looks more like a liverwort when only the gametophyte is present. I hope that additional occurrences of this relatively rare genus can be located in the Pacific Northwest. Having the genus illustrated here should be a good first step for others to seek it out.

I strongly recommend this new field guide to all botanists with an interest in learning more about our non-flowering plants. As Schofield's book states, liverworts are a remarkable group of plants, and upon closer observation, they make a considerable contribution to forest ecosystems, especially in the temperate rain forests along the coast of western North America. At \$25.00 this guide is a good investment. Will you be able to key every liverwort to species with this field guide? Absolutely not. But, having the genus properly identified will speed up considerably the time to do so in more detailed bryofloras. This field guide is a wonderful introduction to recognizing genera of liverworts in Pacific North America. In short order you will be able to recognize the common liverwort genera on rotten wood and logs, soil and humus, tree trunks, rock outcrops and even those liverworts submerged in springs and streams. I recommend it to botanists, ecologists, foresters, and conservation biologists without any reservations.

—JAMES R. SHEVOCK, Research Associate, Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599.



## PRESIDENT'S REPORT FOR VOLUME 49

I am pleased to report that 2002 was a year of accomplishment for the California Botanical Society, thanks to the dedicated efforts of the Editors and Council. Editor John Callaway skillfully concluded his first year in charge of *Madroño*, with four excellent issues completed. The quality, breadth, and depth of articles published in *Madroño*, Volume 49, testifies to the vibrancy of our journal and the effectiveness of John's editorship. Thank you, John! I also thank our Book Editor Jon Keeley, Noteworthy Collection Editors Dieter Wilken and Margriet Wetherwax, and the Board of Editors for their important contributions to Volume 49.

Visibility of articles in *Madroño* was enhanced considerably in 2002 by internet access to titles and abstracts for new issues of the journal through the California Botanical Society web-site ([www.calbotsoc.org](http://www.calbotsoc.org)). John Callaway and Society web-master Curtis Clark worked with Allen Press to provide direct links to contents of *Madroño* (beginning with Vol. 49, issue 1) via Allen Press's APT Online. The results of their efforts will help to increase citation and impact of articles in *Madroño* across the international botanical community.

Over the last year, web-masters Curtis Clark and John LaDuke have made other major improvements to the Society web-site ([www.calbotsoc.org](http://www.calbotsoc.org)), which has become our main clearinghouse for information about publishing in *Madroño* and about society activities, events, and membership. Curtis and John developed a new, streamlined organization for the site, which is easily negotiated with well-placed links. The site also contains links to other societies, institutions, and resources of importance to western North American botany. Many thanks, Curtis and John!

Thanks to efforts by Corresponding Secretary Sue Bainbridge and Treasurer Roy Buck, the Society can now accept credit-card payment for membership dues, using either the web-site membership forms (for new and renewing members) or renewal envelopes sent with the third issue of *Madroño* each year. We trust that the convenience of using a credit card will encourage timely renewal of memberships, which remains an urgent need for the Society. Thanks very much to those members who responded quickly to their renewal notices. For those who have not yet responded, please send your renewals in time for receipt on 28 February 2003. Timely renewal of membership saves the Society considerable expenditure of effort (although late renewal is far better than a lapse in membership).

Significant growth of our membership base would allow the Society to do more to promote botanical research and education. Toward that end, please continue to encourage your colleagues to join us and to publish in *Madroño*. Also, you can help to support botanical research in economically depressed, developing countries by giving a

sponsoring membership or subscription to a foreign scientist or scientific institution or by donating unused copies of *Madroño*. For more information on making such a gift, please contact Corresponding Secretary Sue Bainbridge ([suebain@sscl.berkeley.edu](mailto:suebain@sscl.berkeley.edu)).

Fall 2002 saw outstanding lectures at our monthly meetings in Berkeley by Martin Bidartondo, Truman Young, and Randy Jackson, and we look forward to presentations by distinguished scientists David Ackerly, Kim Steiner, Todd Dawson, and Marcel Rejmanek in winter and spring of 2003. I am indebted to outgoing First Vice-President Rod Myatt for his successful efforts, once again, at assembling such a fine lecture series for the Society's program year. Attendance at our monthly meetings has been strong again this year and I encourage those of you who have an opportunity to participate to please join us, bring a friend, and inform your colleagues about upcoming lectures.

I also strongly encourage our members to attend the Society's biennial graduate student meeting and annual banquet at the University of San Diego on Saturday, 15 February 2003. At the graduate student meeting, held during the day, students from different institutions will be presenting their research proposals, research-in-progress, or completed research in botany in a standard scientific-meeting format. We look forward to a stimulating day of research ideas and results from the promising, next generation of botanists. In the evening, at the annual banquet, we will have the great pleasure of hearing from renowned Baja floristician and cactus expert Dr. Jon Rebman, who will be presenting an after-dinner lecture on recent floristic discoveries in Baja California, Mexico. Jon's expeditions to remote, beautiful, and under-explored regions of Baja California, in collaboration with Mexican scientists, are fine examples of American/Mexican cooperation and accomplishment in science. Thanks very much to Second Vice-President Michael Mayer for planning and organizing the upcoming banquet and to Graduate Student Representatives Robert Lauri and Elizabeth Zacharias for coordinating and conducting the graduate student meeting.

Last, but by no means least, I thank Recording Secretary Staci Markos and Council Members Jim Shevock, Dean Kelch, and Anne Bradley for their dedicated commitment and contributions to furthering the goals of the Society, and to all of our members for your continuing support and participation in the Society's activities and events and for choosing to submit your botanical manuscripts to *Madroño*. This is my last year as President of the Society and I especially thank all of you for making this experience so enjoyable and rewarding for me. Have a great year in 2003!

—BRUCE G. BALDWIN  
December 2002

## EDITOR'S REPORT FOR VOLUME 49

This report serves to inform the members of the California Botanical Society of the status of *Madroño*, from the number of manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 49[4]), the journal has received 61 manuscripts for review, including Articles, Notes, and Noteworthy Collections; 31 of these manuscripts have been accepted for publication in that same time period. The average time for article submission to publication remains at approximately six months. Accepted manuscripts are typically published within approximately three to four months. Few manuscripts were rejected after review; authors of *Madroño* articles did a fine job of responding to reviewers' suggestions.

Over the past five years, there has been a substantial effort to get *Madroño* back on its regular publication schedule, and we are now very close to being on schedule, with six issues published in 2002 (three from volume 48 and three from volume 49). Kristina Schierenbeck (editor of volumes 45–48) deserves most of the credit for this, as she put in an enormous effort to get the journal back on schedule. In addition to catching up on our publication schedule, other improvements have been made with the journal. As noted by Bruce Baldwin in his President's Report, abstracts of *Madroño* are now available on-line via the California Botanical Society's web-site ([www.calbotsoc.org](http://www.calbotsoc.org)). In addition the web-site will soon have more detailed Instructions for Authors for *Madroño* man-

uscripts. With volume 49 we initiated a new policy, encouraging authors to submit names of two to four potential reviewers for manuscripts. If readers have suggestions for other improvements for the journal please let me know.

I want to thank the many people who make *Madroño* possible and who have been incredibly helpful in editing the journal: Kristina Schierenbeck, who gave me lots of help in taking over the editorship and has always been there to answer my questions about the journal; Bruce Baldwin and other members of the CBS Executive Council, who are always extremely helpful and supportive of everything related to *Madroño*; Dieter Wilken and Margriet Wetherwax, who handle all of the reviews for Noteworthy Collections (and without whom the Noteworthy Collections would not be possible); Jon Keeley, who does all of the book reviews; Steve Timbrook, who provides the annual index of *Madroño* articles and the annual table of contents; the Board of Editors, who have provided input and advice whenever I've asked (especially Norm Ellstrand and Carla D'Antonio, who are finishing their terms this year); Annielaurie Seifert at Allen Press, who has been extremely helpful when any editorial question arises; the College of Arts and Sciences at the University of San Francisco, who support my efforts on *Madroño*; and most of all the *Madroño* authors, who continue to submit outstanding manuscripts, and the reviewers (see the accompanying list of reviewers), who put in a substantial effort to improve the quality of manuscripts that *Madroño* publishes.

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DEDICATION



Donald R. Kaplan

Donald R. Kaplan, Professor in the Department of Plant and Microbial Biology at UC Berkeley, has made exceptional contributions to research and education in the field of plant morphology over the last four decades. He received his B.A. in Biology in 1960 from Northwestern University and his Ph.D. in Botany from the University of California, Berkeley in 1965. His dissertation research, on “Floral morphology and reproduction in certain members of the genus *Downingia* (Campanulaceae; Lobelioideae)” marked the beginning of an illustrious career that continues to this day. Don joined the UC Berkeley faculty in 1968, where he established himself as an outstanding researcher, mentor, and educator. He has always tried to blur the boundary between research and teaching. According to Don, “I am a better teacher because I do research . . . similarly, being a teacher gives my research a better perspective and helps me to place the more detailed aspects of what I do in the broader context of knowledge in my field.”

Don’s focus has been on the developmental basis

that underlies the diversity of plant form. He has sought to move away from the traditional approach of plant morphology as a systematic survey of major groups in the plant kingdom. Instead, he has promoted the approach of integration and analysis of key concepts in morphology. His successful efforts have been well recognized. In 1998, he received the Jeannette Siron Pelton Award from the Botanical Society of America (BSA) for his sustained and creative contributions in experimental plant morphology. In addition, Don also received the Alexander von Humboldt Distinguished Senior U.S. Scientist Award.

In citing Don for the Jeannette Siron Pelton Award, the BSA noted that “he has reached out both to traditional plant biologists as well as to those who have come to plant biology through an interest in molecular aspects of biology. He is the author of numerous substantive publications on leaf development that are recognized as classic papers on the subject.” He also has completed influential work evaluating the relationship of cells to

organisms in plants. This work has forced botanists and geneticists to "reevaluate their thinking about the underlying mechanisms responsible for the origin of plant form." His review of the science and history of plant morphology, going back to its origins with Goethe in the late 1700s, which is based on his acceptance speech for the Jeannette Siron Pelton Award, was published in the October 2001 issue of the *American Journal of Botany* (88: 1711–1741).

Don has trained a large number of graduate students, many who have gone on to very productive careers in plant morphology. He has reached an even larger number of aspiring young scientists through his courses, which have drawn high praise from generations of Berkeley's undergraduates and graduate students. Don brings to the classroom an enthusiastic and innovative approach to the subject of plant form and inspires his students with his insatiable curiosity about the biological world. As

one student remarked about Don's class on plant morphology, "the course is a must-have for any serious student of botany. One should not pass up the opportunity to learn from Dr. Kaplan." Another student noted that "Dr. Kaplan is one of the people I've met in academia that has influenced and inspired me the most, both as a researcher and as a teacher." His outstanding teaching was recognized in 1976 when he received the campus-wide Distinguished Teaching Award at UC Berkeley.

His teaching has also led to the development of a multi-volume text, entitled "Principles of Plant Morphology." This book has been the primary focus of Don's recent work. We look forward to its completion and the insight that it will bring to current and future students of plant morphology. In the spirit of his true devotion to plant biology through outstanding research and inspiring teaching, we dedicate volume 49 of *Madroño* to Donald R. Kaplan.



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